Universidad de Alcalá
COMISIÓN DE ESTUDIOS OFICIALES
DE POSGRADO Y DOCTORADO

ACTA DE EVALUACIÓN DE LA TESIS DOCTORAL

(FOR EVALUATION OF THE ACT DOCTORAL THESIS)

Año académico (*academic year):* 2018/19

DOCTORANDO *(candidate PHD)*: **RODRIGUEZ GARCIA, LAURA**
D.N.I./PASAPORTE (*Id.Passport*): ******9137M**
PROGRAMA DE DOCTORADO *(Academic Committee of the Programme)*: **D413-ECOLOGÍA. CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS**
DPTO. COORDINADOR DEL PROGRAMA *(Department)*: **CIENCIAS DE LA VIDA**
TITULACIÓN DE DOCTOR EN *(Phd title)*: **DOCTOR/A POR LA UNIVERSIDAD DE ALCALÁ**

En el día de hoy 31/05/19, reunido el tribunal de evaluación, constituido por los miembros que suscriben el presente Acta, el aspirante defendió su Tesis Doctoral **con Mención Internacional** (*In today assessment met the court, consisting of the members who signed this Act, the candidate defended his doctoral thesis with mention as International Doctorate)*, elaborada bajo la dirección de (*prepared under the direction of)* MARIA DEL BREZO MARTINEZ DIAZ-CANEJA // FERNADO TUYA CORTES.

Sobre el siguiente tema *(Title of the doctoral thesis)*: *TROPICAL CORALS UNDER CLIMATE CHANGE: UNRAVELLING ECOLOGICAL INSIGHT FROM VARYING METHODOLOGICAL STRATEGIES*

Finalizada la defensa y discusión de la tesis, el tribunal acordó otorgar la CALIFICACIÓN GLOBAL[1] de **(no apto, aprobado, notable y sobresaliente)** *(After the defense and defense of the thesis, the court agreed to grant the GLOBAL RATING (fail, pass, good and excellent)*: SOBRESALIENTE

Alcalá de Henares, a 31 de mayo de 2019

Fdo. *(Signed)*: JUAN JUNOY

Fdo. *(Signed)*: Rosa M. Chegaoui

Fdo. *(Signed)*: Sabrina Clemente Martín

FIRMA DEL ALUMNO (candidate's signature),

Fdo. *(Signed)*: .....

Con fecha 24 de junio de 2019 la Comisión Delegada de la Comisión de Estudios Oficiales de Posgrado, a la vista de los votos emitidos de manera anónima por el tribunal que ha juzgado la tesis, resuelve:

☒ Conceder la Mención de "Cum Laude"
☐ No conceder la Mención de "Cum Laude"

La Secretaria de la Comisión Delegada

[1] La calificación podrá ser "**no apto**" "**aprobado**" "**notable**" y "**sobresaliente**". El tribunal podrá otorgar la mención de "cum laude" si la calificación global es de sobresaliente y se emite en tal sentido el voto secreto positivo por unanimidad. (*The grade may be "**fail**" "**pass**" "**good**" or "**excellent**". The panel may confer the distinction of "cum laude" if the overall grade is "Excellent" and has been awarded unanimously as such after secret voting.).*

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En aplicación del art. 14.7 del RD. 99/2011 y el art. 14 del Reglamento de Elaboración, Autorización y Defensa de la Tesis Doctoral, la Comisión Delegada de la Comisión de Estudios Oficiales de Posgrado y Doctorado, en sesión pública de fecha 24 de junio, procedió al escrutinio de los votos emitidos por los miembros del tribunal de la tesis defendida por ***RODRIGUEZ GARCIA, LAURA***, el día 31 de mayo de 2019, titulada, *TROPICAL CORALS UNDER CLIMATE CHANGE: UNRAVELLING ECOLOGICAL INSIGHT FROM VARYING METHODOLOGICAL STRATEGIES* para determinar, si a la misma, se le concede la mención "cum laude", arrojando como resultado el voto favorable de todos los miembros del tribunal.

Por lo tanto, la Comisión de Estudios Oficiales de Posgrado y Doctorado **resuelve otorgar** a dicha tesis la

MENCIÓN "CUM LAUDE"

Alcalá de Henares, 24 de junio de 2019
EL VICERRECTOR DE INVESTIGACIÓN Y TRANSFERENCIA
F. Javier de la Mata de la Mata

Copia por e-mail a:
Doctorando: RODRIGUEZ GARCIA, LAURA
Secretario del Tribunal: SABRINA CLEMENTE MARTIN
Directores de Tesis: MARIA DEL BREZO MARTINEZ DIAZ-CANEJA // FERNANDO TUYA CORTES

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DILIGENCIA DE DEPÓSITO DE TESIS.

Comprobado que el expediente académico de D./Dª LAURA RODRIGUEZ GARCIA reúne los requisitos exigidos para la presentación de la Tesis, de acuerdo a la normativa vigente, y habiendo presentado la misma en formato: ☒ soporte electrónico ☐ impreso en papel, para el depósito de la misma, en el Servicio de Estudios Oficiales de Posgrado, con el nº de páginas: 175 se procede, con fecha de hoy a registrar el depósito de la tesis.

Alcalá de Henares a 13 de MARZO de 20 19

Pilar de la Vega

Fdo. El Funcionario

Tropical corals under climate change: unravelling ecological insight from varying methodological strategies - 2019

Laura Rodríguez García

Universidad de Alcalá

Programa de Doctorado en
Ecología, Conservación y Restauración de Ecosistemas

TROPICAL CORALS UNDER CLIMATE CHANGE: UNRAVELLING ECOLOGICAL INSIGHT FROM VARYING METHODOLOGICAL STRATEGIES

Tesis Doctoral presentada por

LAURA RODRÍGUEZ GARCÍA

2019

Universidad de Alcalá

Programa de Doctorado en "Ecología, Conservación y Restauración de Ecosistemas" (D330)

UNIVERSIDAD DE ALCALÁ, PATRIMONIO DE LA HUMANIDAD

TROPICAL CORALS UNDER CLIMATE CHANGE: UNRAVELLING ECOLOGICAL INSIGHT FROM VARYING METHODOLOGICAL STRATEGIES

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Directores:

Dr. María del Brezo Martínez Díaz-Caneja

Dr. Fernando José Tuya Cortés

Alcalá de Henares, marzo 2019

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

Dr. Fernando Tuya Cortés, con DNI [redacted], Profesor Titular del Departamento de Biología de la Universidad de Las Palmas de Gran Canaria,

CERTIFICA:

Que los trabajos de investigación incluidos en la memoria de tesis doctoral titulada: "Tropical corals under climate change: unravelling ecological insight from varying methodological strategies" han sido realizados bajo mi supervisión y están aptos para ser presentados por la Licenciada Doña Laura Rodríguez García ante el tribunal que en su día se constituya, para aspirar al grado de Doctor en el programa de doctorado de Ecología, conservación y restauración de ecosistemas de la Universidad de Alcalá.

Y para que surja los efectos oportunos, firmo en Las Palmas de Gran Canaria, a 19 de febrero de 2019.

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CERTIFICA:

Que los trabajos de investigación incluidos en la memoria de tesis doctoral titulada: "Tropical corals under climate change: unravelling ecological insight from varying methodological strategies" han sido realizados bajo mi supervisión y están aptos para ser presentados por la Licenciada Doña Laura Rodríguez García ante el tribunal que en su día se constituya, para aspirar al grado de Doctor en el programa de doctorado de Ecología, conservación y restauración de ecosistemas de la Universidad de Alcalá.

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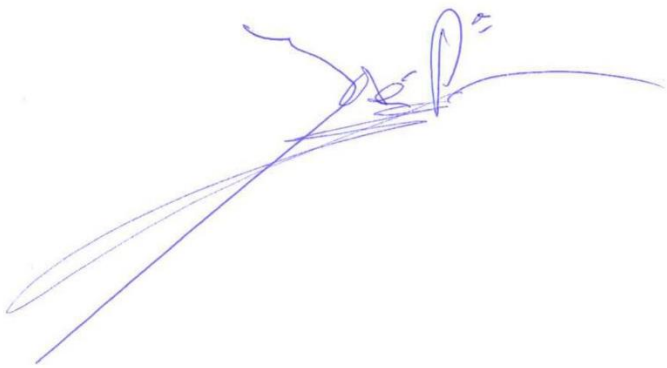
JOSÉ Mª REY BENAYAS, Catedrático de Ecología en la Universidad de Alcalá y Tutor de la presente Tesis doctoral,

INFORMA:

Que el trabajo descrito en la presente memoria, titulado "TROPICAL CORALS UNDER CLIMATE CHANGE: UNRAVELLING ECOLOGICAL INSIGHT FROM VARYING METHODOLOGICAL STRATEGIES", ha sido realizado bajo su tutorización dentro del Programa de Doctorado Ecología. Conservación y Restauración de Ecosistemas (RD 99/2011), adscrito al Departamento de Ciencias de la Vida de la Universidad de Alcalá. Esta tesis reúne todos los requisitos propios de este tipo de trabajo: rigor científico, aportaciones novedosas y aplicación de una metodología adecuada. Por lo tanto, doy mi Visto Bueno a la presentación de dicha Tesis Doctoral.

Alcalá de Henares, 19 de febrero de 2019



Universidad de Alcalá

D. MIGUEL ÁNGEL DE ZAVALA GIRONÉS, Coordinador de la Comisión Académica del Programa de Doctorado en ECOLOGÍA, CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS,

INFORMA que la Tesis Doctoral titulada TROPICAL CORALS UNDER CLIMATE CHANGE: UNRAVELLING ECOLOGICAL INSIGHT FROM VARYING METHODOLOGICAL STRATEGIES, presentada por D/Dª **LAURA RODRÍGUEZ GARCÍA,** bajo la dirección del Dr. Mª del BREZO MARTÍNEZ-DÍAZ CANEJA / de la Dr/a. FERNANDO TUYA CORTÉS, reúne los requisitos científicos de originalidad y rigor metodológicos para ser defendida ante un tribunal. Esta Comisión ha tenido también en cuenta la evaluación positiva anual del doctorando, habiendo obtenido las correspondientes competencias establecidas en el Programa.

Para que así conste y surta los efectos oportunos, se firma el presente informe en Alcalá de Henares a 06 de Marzo de 2019.

Fdo.: Miguel Ángel de Zavala Gironés

A mis padres (Abel y Leonor)

"During this crossing, the sea continually lavished us with the most marvelous sights. Its variety was infinite. It changed its setting and decor for the mere pleasure of our eyes […] I immediately recognized the wondrous region in which Captain Nemo did the honors that day. ***It was the coral realm****.*

In the zoophyte branch, class Alcyonaria, one finds the order Gorgonaria, which contains three groups: sea fans, isidian polyps, and coral polyps. It's in this last that precious coral belongs, an unusual substance that, at different times, has been classified in the mineral, vegetable, and animal kingdoms. Medicine to the ancients, jewelry to the moderns, it wasn't decisively placed in the animal kingdom until 1694, by Peysonnel of Marseilles.

A coral is a unit of tiny animals assembled over a polypary that's brittle and stony in nature. These polyps have a unique generating mechanism that reproduces them via the budding process, and they have an individual existence while also participating in a communal life. Hence they embody a sort of natural socialism.

I was familiar with the 'latest' research on this bizarre zoophyte-- which turns to stone while taking on a tree form, as some naturalists have very aptly observed-- and nothing could have been more fascinating to me than to visit one of these petrified forests that nature has planted on the bottom of the sea."

Jules Verne*.* ***Twenty Thousand Leagues Under the Sea, 1869****.*

Photo: L. Rodríguez

"The nature of life is not permanence but flux." - D. A.

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Acknowledgments/Agradecimientos

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Photo: L. Rodríguez

Abstract

Tropical coral reefs are one of the most diverse ecosystems on Earth. However, their main structural components, i.e. corals (scleractinian and hydrocorals), are highly threaten by climate change and local perturbations. Climate change is altering corals distributions worldwide, and predictions of corals habitat suitability, based on the IPCC climatic scenarios, can help to early detect range contractions and expansions. This thesis aims to predict these potential distributional changes. To accomplish this goal, the main environmental factors driving corals distribution are explored. Then, modelling techniques as 'Species Distribution Models' are used to predict current and future corals habitat suitability. However, future climatic scenarios usually represent conditions that do not exist in the current world, and extrapolations are needed. Corals currently live close to their upper thermal tolerance thresholds, and their response curves are truncated; thus, the detection of their future habitat decline is a challenge. In this thesis, a new Hybrid method, integrating the complete physiological response of a hydrocoral into a correlative model, is proposed. The hybrid model eliminates the uncertainty of extrapolations and allows robust predictions, detecting future corals habitat suitability declines, undetected by classical methods. Additionally, this thesis explores potential future changes in the richness, phylogenetic diversity and phylogenetic species variability of Atlantic coral communities; this information is key to select the most important areas and species for conservation purposes. Lastly, this thesis resolves the genetic relationships of a hydrocoral and its symbionts on both sides of the Atlantic. Results demonstrated a genetic mismatch between the coral host and their symbionts, which clears up an adaptation strategy to climate change by acquiring new symbionts from the environment, or by shuffling their internal symbionts density depending on environmental conditions. In conclusion, this thesis contributes to an integrative knowledge, based on different methodological approaches, to explore the most relevant ecological responses of tropical corals under climate change scenarios.

Resumen en español

Antecedentes

El cambio climático ha provocado, entre otros efectos, el aumento medio de la temperatura global. Estos incrementos de temperatura han inducido a su vez, importantes cambios en los ecosistemas marinos, como son los cambios en la distribución de las especies. Uno de los grupos animales más amenazados frente al calentamiento global son los corales tropicales (scleractinia e hidrocoral). Estos organismos son los principales componentes estructurales de los arrecifes de coral, uno de los ecosistemas más diversos del planeta. Los corales son especies pioneras que proporcionan hábitat para otros organismos, además de multitud de servicios ecosistémicos. Son animales coloniales, compuestos por pólipos, y en el mayor de los casos, endosimbiontes que realizan la fotosíntesis aportando nutrientes a sus hospedadores. El cambio climático, junto con impactos antropogénicos locales, como aumentos de la sedimentación o fertilización, están provocando la migración y desaparición de los corales a un ritmo acelerado, con graves implicaciones ecológicas para todo el medio marino.

Objetivos y metodología

El objetivo de esta tesis es predecir posibles expansiones y contracciones en el hábitat de corales e hidrocorales tropicales a escalas oceánicas, en concreto en el océano Indo-Pacífico (Capítulo 2) y en el Atlántico (Capítulos 3 y 4). Con esta tesis se espera, por tanto, ampliar el conocimiento sobre los factores ambientales que afectan a la distribución de los corales; y predecir potenciales cambios en su distribución, según distintos escenarios de cambio climático predichos por el Panel Intergubernamental de Cambio Climático (IPCC) (Capítulos 2, 3 y 4). Se pretende, a su vez, predecir las posibles consecuencias de estos cambios sobre la diversidad de la comunidad de corales. Para ello, se plantea el uso de modelos de distribución de especies (SDMs) (Capítulos 2, 3 y 4). Los SDMs pueden servir como herramienta de apoyo para la clasificación de especies que *a priori* no son consideradas como amenazadas. Como p. ej. *Pavona varians*, coral categorizado por la UICN como de "Preocupación Menor" y conocido por ser una especie oportunista resistente al estrés ambiental; pero que según las predicciones puede verse negativamente afectado por el cambio climático (Capítulo 2). Debido a la limitación de los SDMs para poder realizar extrapolaciones en ambientes futuros no análogos, como por ejemplo temperaturas futuras más cálidas que las actuales, se propone un nuevo método, denominado híbrido. Este método integra la respuesta fisiológica de un hidrocoral

frente a un gradiente térmico completo (incluyendo valores letales futuros), como una variable más dentro del modelo correlativo clásico (Capítulo 4). Con el objetivo de predecir cambios en la diversidad filogenética de las comunidades de corales del Atlántico, se combinaron los resultados de los SDMs (transformándolos en matrices de composición de especies) con distintos análisis filogenéticos, p. ej. la diversidad filogenética (PD) y la variabilidad filogenética de las especies (PSV) (Capítulo 3). Esta información puede ser aplicada para el diseño de estrategias de conservación. Por último, se establecieron las relaciones filogenéticas, a partir de marcadores moleculares, entre un hidrocoral (*M. alcicornis*) y sus simbiontes, para determinar posibles patrones de origen y dispersión a ambos lados del Océano Atlántico, así como los procesos ecológicos de adaptación al medio (Capítulo 5). Todas estas metodologías tienen como objetivo final proporcionar herramientas de detección temprana de los posibles impactos del cambio climático en los corales, lo que puede ayudar a establecer estrategias de conservación.

Resultados e implicaciones

Las variables más relevantes que determinaron la distribución de los corales estudiados en esta tesis fueron: la temperatura de la superficie del mar, la salinidad, la atenuación difusa de la columna de agua, la nubosidad, la radiación fotosintéticamente activa, el pH y el fosfato. La importancia de estas variables puede variar en función de la especie y la escala de estudio. En cuanto a las predicciones futuras sobre la distribución del coral Indo-Pacífico *Pavona varians*, el modelo predijo una disminución masiva en todas sus áreas para el año 2100. Este resultado sirve de alerta sobre futuras amenazas no tenidas en cuenta hasta el momento, incluso en especies *a priori* resistentes. También, se espera que el hidrocoral *Millepora alcicornis*, así como la mayoría de los corales tropicales del Atlántico, sufran retracciones en su rango de distribución en latitudes bajas, donde las temperaturas futuras excederán los umbrales térmicos de las especies. Sin embargo, dichas especies expandirán su rango a latitudes más altas, debido al esperado aumento de temperatura en latitudes templadas. Los cambios futuros en la distribución de corales Atlánticos también producirán cambios en la diversidad filogenética de sus comunidades. Estos cambios aparecen distribuidos de manera aleatoria a lo largo de la filogenia. La diversidad filogenética aumentará en ciertas zonas más templadas y frías, y decaerá en zonas cálidas, sobre todo en zonas del Caribe que actualmente se ven afectadas por episodios de blanqueamiento. Las especies pertenecientes a clados aislados (elevada

diferenciación evolutiva) contribuyen a notorios aumentos o descensos en la diversidad filogenética y en la variabilidad filogenética de las especies, convirtiéndolas en especies clave para la conservación del ecosistema. Con respecto al nuevo modelo Híbrido, este produjo predicciones más realistas que las del modelo correlativo, permitiendo proyecciones sin extrapolaciones al añadir el predictor fisio-climático. También, incorporó restricciones en la idoneidad del hábitat por parte de otros predictores, como la salinidad, ausentes en el modelo fisiológico, pero de los que se tenía información correlativa. En relación a los análisis genéticos de las poblaciones de *M. alcicornis* y sus simbiontes, se encontró una elevada variación genética 'entre' y 'dentro' de las poblaciones estudiadas a ambos lados del Atlántico. Se determinó que el origen genético de las colonias establecidas en las Islas Canarias fue el Caribe (Atlántico Oeste); sin embargo, sus simbiontes estaban genéticamente más relacionados con los simbiontes de las Islas de Cabo Verde (Atlántico Este). Esta discrepancia sugiere que *M. alcicornis* puede poseer la capacidad de adquirir simbiontes a través del medio (transmisión horizontal), o bien que, varios tipos de simbiontes cohabiten en la misma colonia cambiando su densidad en función de las condiciones ambientales.

Conclusiones

Como consecuencia del cambio climático, la mayoría de los corales tropicales sufrirá contracciones en sus rangos de distribución en latitudes bajas donde las temperaturas futuras excederán los valores máximos de tolerancia térmica de los corales. A su vez, éstos expandirán su área a latitudes mayores, en búsqueda de refugios frente al calentamiento global. La posible pérdida futura de corales del Atlántico se distribuirá aleatoriamente a lo largo de la filogenia, aliviando así la posible pérdida de linajes únicos. La integración de información fisiológica en los denominados modelos Híbridos mejora la transferibilidad de los modelos, lo que da como resultado mejores predicciones futuras. Permite detectar áreas de extinción en condiciones climáticas que no existen en la actualidad, y que de otro modo pasarían desapercibidas, como ocurre con las predicciones de los modelos correlativos clásicos. Por ende, estos modelos híbridos son herramientas útiles y aconsejables para el apoyo en la toma de decisiones de los planes de conservación. El uso de marcadores moleculares nos proporciona información sobre las relaciones genéticas entre poblaciones separadas por miles de kilómetros. Además, nos ayuda a entender mecanismos de adaptación de los corales al cambio climático. La implementación de muestreos sistemáticos globales para el censo de corales, la actualización

y mantenimiento de un inventario de secuencias de ADN, así como la realización de estudios fisiológicos exhaustivos de estas especies; proporciona información necesaria para estimar la biodiversidad de los corales a distintas escalas espaciales y temporales, lo cual es esencial para proteger a estos ecosistemas. La combinación de distintas aproximaciones ecológicas, como los SDMs, los análisis genéticos y los filogenéticos permite una visión integradora y útil para el estudio ecológico de los corales, lo cual constituye la base para su gestión y conservación.

Abbreviations

- **AIC**: Akaike Information Criterion
- **AUC**: area under the curve
- **BPP**: Bayesian posterior probability
- **Chl**: Chlorophyll
- **CMIP**: Coupled Model Intercomparison Project
- **COI**: Cytochrome Oxidase Subunit I
- **Da**: Diffuse attenuation at 490 mm (m^{-1}) of the water column
- **Dissox**: Dissolved Oxygen
- **DMSO**: Dimethyl Sulfoxide
- **ED**: evolutionary distinctiveness
- **EMODnet**: European Marine Observation Data Network
- **Fv/Fm**: maximal quantum yield of photosynthesis
- **GBIF**: Global Biodiversity Information Facility
- **GLM**: Generalized Linear Model
- **Icong**: congruence index
- **IPCC**: Intergovernmental Panel on Climate Change
- **ITS**: internal transcribed spacer
- **IUCN**: International Union for Conservation of Nature
- **LSU**: Large-Subunit
- **MaxEnt**: Maximum Entropy Modelling Software
- **MCMC**: Markov Chain Monte Carlo
- **MEGA**: Molecular Evolutionary Genetic Analysis
- **MoD**: most dissimilar variable
- **OBIS**: Ocean Biogeographic Information System
- **PAM**: pulse amplitude modulated
- **PAR**: Photosynthetically Available Radiation
- **PCR**: polymerase chain reaction
- **PD**: Faith's Phylogenetic Diversity
- **PD_{SES}**: standardized PD
- **pH**: ocean acidity
- **PSRF**: potential scale reduction factor
- **PSV**: Phylogenetic species variability
- **rDNA**: ribosomal deoxyribonucleic acid
- **RF**: Random Forest
- **RFLP**: Restriction Fragment Length Polymorphism
- **ROC**: Receiver Operating Characteristic
- **SDM**: Species Distribution Model
- **SST**: Sea Surface Temperature
- **VIF**: Variance inflation factor
- **WoRMS**: World Register of Marine Species

Chapter 1: General Introduction

1.1. The impact of climate change on marine ecosystems

Climate has changed throughout geologic time (throughout the 4.6-billion-year history of the Earth), and the evolution of life has been directly connected with these changes. However, an accelerated climate change has occurred over the last century due to increases of anthropogenic CO2 emissions. The average temperature of Earth has increased approximately 1ºC above preindustrial levels (IPCC Special Report 1.5 Degrees, 2018). Anthropogenic global warming is increasing at an estimated rate of 0.2°C per decade. These recent climatic changes have been translated into more frequent and acute weather-related events such as storms, hurricanes, heat waves, droughts, forest fires, floods or coral bleaching. The economics effects of climate change are estimated in approximately US $360 billion annually (NOAA, 2018). Ultimately, these aforementioned changes have affected the phenology and physiology of organisms, the distribution of species and the structure of the communities and ecosystems (Walther et al., 2002).

Habitat declines and range shifts, have been registered during the last decades. For example, in butterflies (Parmesan et al., 1999), plants (Pauli, Gottfried, & Grabherr, 1996) or ectotherms (Isaak & Rieman, 2013). But these shifts have not only occurred in terrestrial species affecting terrestrial ecosystems (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), also in the oceans (Hoegh-Guldberg & Bruno, 2010). Heat has influenced the dynamic of ocean currents (Alheit & Bakun, 2010; Hoegh-Guldberg & Bruno, 2010) and has acidified the oceans (Doney, Fabry, Feely, & Kleypas, 2009); and many fishes (Last et al., 2011), marine mammals (Simmonds & Isaac, 2007), kelp forest (Harley et al., 2012; Wernberg et al., 2016) or corals (Yamano, Sugihara, & Nomura, 2011) have suffered severe range contractions, or have been forced to migrate to higher latitudes or deeper waters searching for milder temperatures.

1.2. Coral Reefs: biodiversity and threats (scleractinian corals and hydrocorals)

Reef building corals (scleractinian and hydrocorals) are the main components of coral reefs, one of the most diverse

ecosystems on Earth (Buddemeier, Kleypas, & Aronson, 2004) (Fig. 1). They are pioneering species that provide habitat for many other marine organisms. Stony corals are animals belonging to the phylum Cnidaria and order Scleractinia (Anthozoa: Hexacorallia). Hydrocorals belong the same phylum but to the order Anthoathecata. The family Milleporidae also builds a calcium carbonate skeleton as the scleractinian corals, the species of this family are also known as fire corals due to its sting nematocysts (Lewis, 2006). Approximately one third of corals are gonochoric (have separate sexes) where the rest are hermaphrodites (polyps are both male and female). These organisms can rapidly growth though asexual reproduction when small fragments are detached from the mother colony. However, sexual reproduction can be different among species. Some species are broadcast spawners which means they only spawn during one annual mass spawning event. Gametes (eggs and sperm) are resealed into the water where fertilization and development occur, and then the fertilised embryos and the planula spend some time searching for the proper substrate to settle. On the other side, other corals are brooder specialists. In this case, an internal fertilization and embryogenesis occurs inside the gastrovascular cavity of the polyp before the release of large larvae during multiple events synchronised by the moon cycle. The settlement and posterior metamorphosis to coral polyps usually occur straight after the release of the planulae. Regarding the sexual reproduction of hydrocorals from the *Millepora* genera, they are broadcast spawners with gonochoristic colonies (Lewis, 2006). These organisms produce ampullae (cavities on the surface of the coenosteum) containing the medusae where the games are grown. Male and female medusae with natatory capacities are released into the water expelling their sperm or oocytes to achieve the fertilization and larva formation (Bourmaud, Leung, Bollard, & Gravier-Bonnet, 2013).

Fig. 1. Underwater image of a coral reef ecosystem. Photo credit: Laura Rodríguez.

Most corals and hydrocorals live in symbiosis with photosynthetic algae, commonly belonged to the Symbiodiniaceae family (LaJeunesse et al., 2018), which provide several benefits to the coral. For example, the photosynthesis produced by these endosymbionts generates carbon products used by the coral to construct its calcium carbonate skeletons, creating the characterising three-dimensional hard structure of an autogenic engineering species. These organic products also contribute to corals feeding, increasing their growth rates. On the other side, the host supplies inorganic nutrients to the symbionts and refuge from herbivores (Weis, Reynolds, deBoer, & Krupp, 2001). This symbiosis is relevant for the survival of tropical coral reefs in a context of climate change. The symbiont acquisition may differ among corals, some of them transmit their symbiont directly to its offspring (vertical transmission); while others acquire it from the environment (horizontal transmission) through phagocytosis (Hirose, Kinzie, & Hidaka, 2001; Stat, Carter, & Hoegh-Guldberg, 2006; Weis et al., 2001) allowing the coral to select the best symbiont from the potential candidates (Fig. 2) (Byler, Carmi-Veal, Fine, & Goulet, 2013). Ultimately others, utilize both strategies, acquiring symbionts through horizontal transmission that are perpetuated via vertical transmission (Byler, Carmi-Veal, Fine, & Goulet, 2013). It is also possible that several symbiont species cohabit in the same colony in different proportions, and environmental changes may produce a shift in the symbiont proportions, e.g.

background symbionts becoming more abundant after an environmental change (Fay & Weber, 2012; Thornhill, LaJeunesse, Kemp, Fitt, & Schmidt, 2006). Nowadays, zooxanthellate corals (i.e. corals living in association with dinoflagellates) are considered as holobionts, taking into account not only the coral polyps but also their associated symbionts (e.g. *Simbiodiniaceae* and another microbiota) (Zlatarski & Stake, 2012).

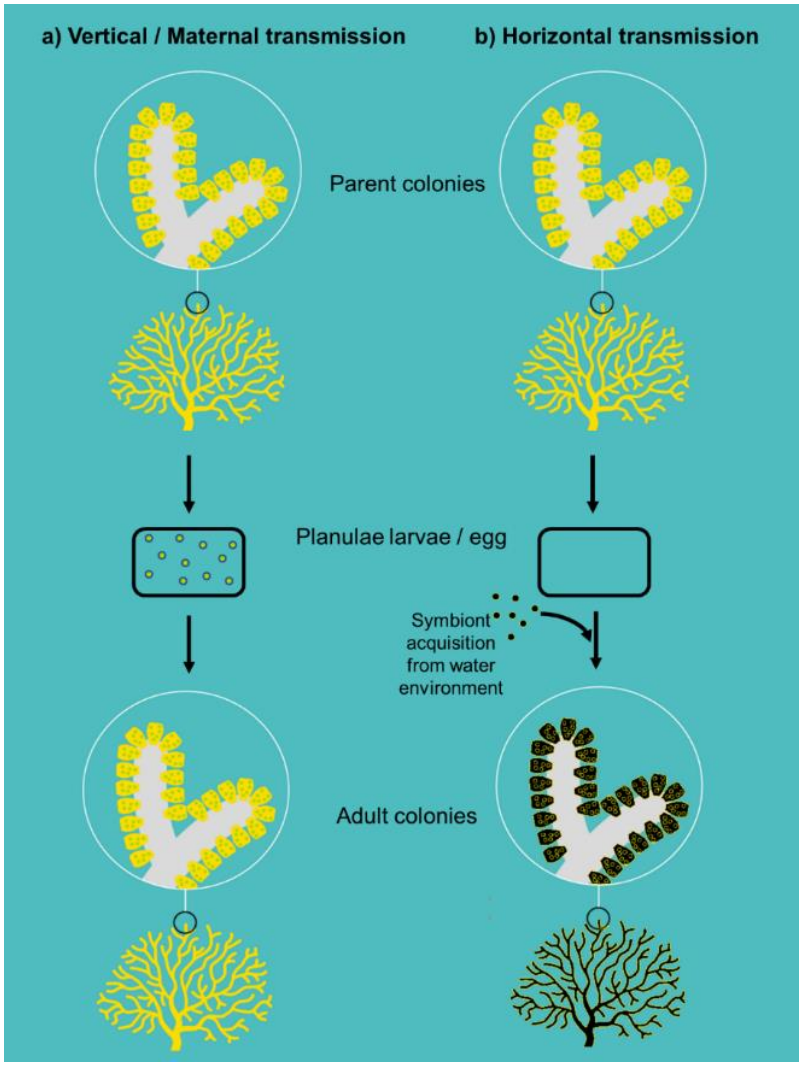

Fig. 2. Symbiont transmission strategies. a) vertical transmission: the parent colony directly transfer the symbionts to the offspring. b) horizontal transmission: the planulae are lack of parents' symbionts and the offspring acquire the new symbionts from the water environment. Figure modified from Stat et al., 2006.

One of the most affected marine ecosystems by climate change effects are tropical Coral Reefs. They are also experiencing contraction and expansion in their habitat ranges (e.g. (L. Hughes, Steffen, & Rice, 2016; Yamano, Sugihara, & Nomura, 2011). Coral reefs provide multitude of ecosystem services through tourism, coastal protection or supplying fish and other marine fauna stocks for human consumption (Spalding, Ravilious, & Green, 2001; Stat et al., 2012). Therefore, any negative impact on them can produce large human, biodiversity and economic losses.

Tropical coral reefs are usually limited to latitudes lower than 30º (tropics) (Fig. 3). Sea water temperature is one of the main factors driving corals distribution (Freiwald, Fosså, Grehan, Koslow, & Roberts, 2004; Gori, Reynaud, Orejas, Gili, & Ferrier-Pagès, 2014). It controls many physiological processes as respiration and calcification that directly affect the normal function of reef building corals (Jokiel & Coles, 1977; Naumann, Orejas, & Ferrier-Pagès, 2014). High temperatures trigger bleaching events, which is the loss of the unicellular algae that lives symbiotically within the polyps (Douglas, 2003), compromising corals' health and ultimately causing death (Fig. 4). Conversely, low temperatures can also produce damages in the photosynthetic apparatus inducing corals' mortality (Coles & Jokiel, 1977; Roth & Deheyn, 2013; Saxby, Dennison, & Hoegh-guldberg, 2003). Aside from temperature, there are other physical and climatic factors driving corals geographic distributions. For example, low photosynthetic active radiation (PAR) levels can restrict corals distribution, particularly at high latitudes where the irradiance limits the photosynthetic activity of the symbiont. In the same way, high turbidity of the water column may also reduce the irradiance penetration in the oceans. As corals have salinity constraints (Ferrier-Pagès et al., 1999; Berkelmans et al., 2012), hyper and hyposalinity conditions may generate regional biogeographic patterns, for example, avoiding estuarine zones (Jokiel et al., 1993). The pH in the oceans is decreasing as a result of the CO2 production by anthropogenic sources (Sabine et al., 2004; Anthony et al., 2008). This reduction is ultimately causing the decalcification of reef building corals by the dissolution of the calcium carbonate present in their skeletons (Eyre et al., 2018; Feely et al., 2004; Ohde & Hossain, 2004). The biochemical component, nitrate, stimulates plankton growth and water turbidity

(Hallock & Schlager, 1986) generating eutrophic waters which are unsuitable for coral reefs. In this sense, high levels of nitrate also increase the severity of coral diseases and bleaching effects and eventually produces a diminution of eggs fertilization (Koop et al., 2001; Fabricius, 2005). Ultimately, high nitrate and phosphate levels may increase the abundance of macroalgae, causing competition against corals (Lapointe, 1997). Changes in these factors may alter the current health and distribution of corals worldwide, so they must be considered when predictions are developed. Distributional shifts are also triggering changes in coral taxonomic and functional compositions, leading to a large decline in biodiversity (Hoey et al., 2016; Stocker, 2014). Over the last decades around one third of the coral reefs have suffered any type of stress causing declines in coral cover or habitat suitability (Carpenter et al., 2008), with recurrent bleaching events during the last years, e.g in the Great Barrier Reef (L. Hughes et al., 2016; T.P. Hughes et al., 2017). But nor only coral declines cause catastrophic effects on tropical marine communities; also coral expansions may produce unpredictable changes in temperate communities. For example, the temperate Australian reef community, typically based on kelp forest, is now being replace by tropical corals, fishes and seaweeds (Wernberg et al., 2016). Therefore, the prediction of climate change effects on corals' distribution is an urgent need to idetify the most threaten areas, and to be able to focus conservation efforts on them.

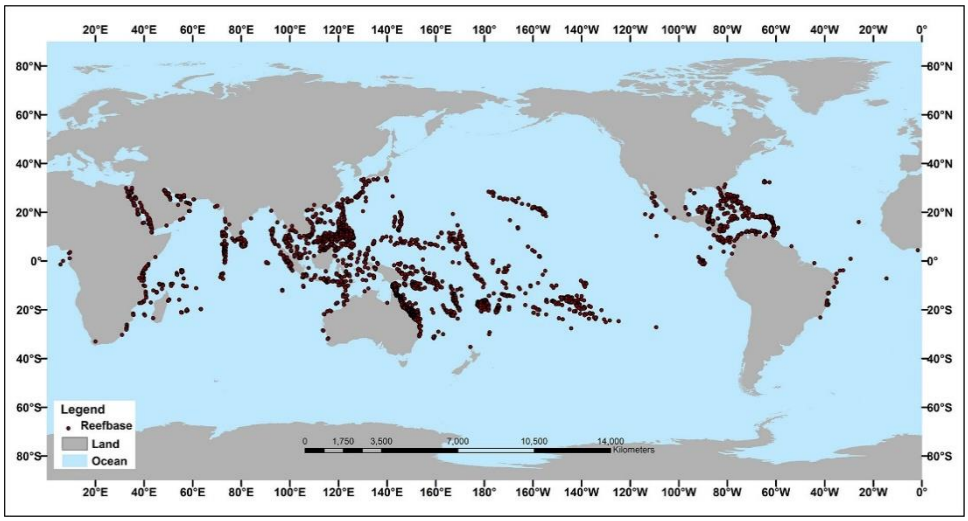

Fig.3. Common distribution of tropical coral reefs in the Oceans. Red points indicate tropical coral reefs locations. Source: National Oceanic and Atmospheric Administration (NOAA).

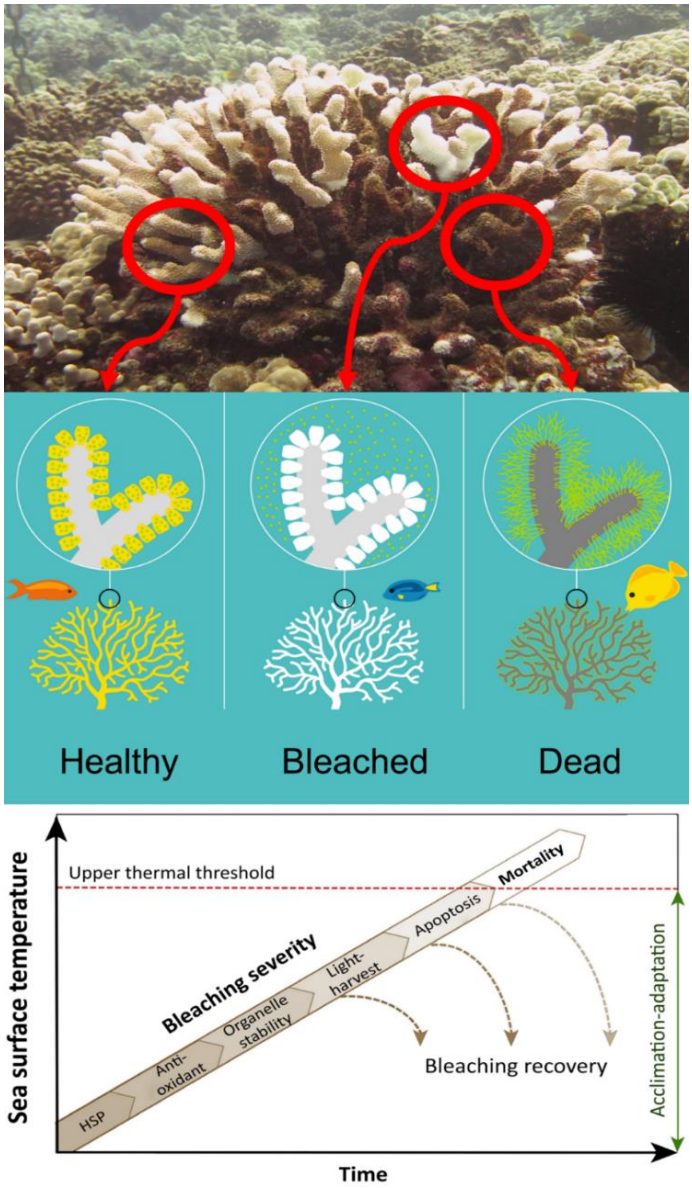

Fig. 4. Up. Scheme of a coral colony with healthy fragments (brown colour due to symbiont pigments), bleached fragments (white colour due to lose of symbionts) and dead fragments (dark brown colour due to the growth of filamentous algae and cyanobacteriain on the dead coral skeleton). Down: the functional response of a coral to thermal stress acrros time. As the sea surface temperatures are raised, the severity of the bleaching process increases too. If the upper thermal threshold is not exceeded, and the temperature deceases across time, the coral can be recovered from bleaching. But if the temperature exceed the upper thermal threshold, the coral dies. Photo credit: Laura Rodríguez. Schemes from NOAA and Suggett et al. (2017).

In the face of these environmental disturbances, some type of corals seem to bear them better than others. Loya et al. (2001) identified that corals' morphology affected bleaching vulnerability; branching corals were more susceptible to bleaching than massive and encrusting corals. Similarly, Darling et al 2012 identified four life history strategies of corals: competitive, weedy, stress-tolerant and generalist taxa. Competitive species are abundant in healthy and productive reefs, but disturbances produce their replacement by weedy (opportunistic) or intermediate (generalist) species. Stress tolerant species are late successional species, with high fertility rates and low growth rates, which can succeed in unproductive conditions. Remarkably, not only coral traits can help corals to face environmental and anthropogenic disturbances; corals endosymbionts can also provide corals with resilience (Putnam, Barott, Ainsworth, & Gates, 2017). For example, the inoculation of symbionts locally adapted to warm temperatures, induce thermal tolerance in corals exposed to high temperatures (32ºC). In contrast, corals inoculated with symbionts from cooler areas, present higher bleaching and mortality rates at the same temperature (Howells et al., 2012). The identification of coral disturbances, the prediction of their potential effects on coral reefs, and the recognition and characterization of the resistence/aclimatation/adaptation capacitities of these organisms, is an urgent need for the conservation of this biodiverse ecosystem. Its conservation will also preserve the rest of the biological entities associated with it, as well as the ecosystem services provided by it.

1.3. Methodological Overview

1.3.1. Study regions

Tropical coral reefs are marine ecosystems restricted to shallow waters, usually occurring at latitudes lower than 30º, with limited nutrient concentrations and warm temperatures. There exist different types of coral reeefs. Fringing reefs, grow parallel the coastlines of islands and continents, separated from the shore by narrow shallow lagoons. Barrier reefs also appear near the coastline but separated by deeper and wider lagoons. Atolls are originated from sunk volcano creaters creating protected lagoons in the middle of the sea. These are the main types or reefs, but other coral entities, such as small patch reefs or solitary corals can also appear in the oceans (Coral Reef Alliance, 2018).

Caribbean reefs, appeared in the formally tropical western Atlantic, include the coral reefs of Florida, The Bahamas, Bermuda, and the northeastern coast of South America as well as those of the Caribbean Sea. Most of them are fringing reef systems with only two considered as barrier reefs (one from south of Mexico to Honduras, and the other in Colombia); approximately just 20 true atolls are present from south of Mexico to Nicaragua (Coral Reef Alliance, 2018). The Greater Caribbean became isolated from the Pacific ~3-4 million years ago by the Isthmus of Panama; since then, it has evolved creating its own unique coral reef biota. However, its coral diversity is much lower, with only 62 stony coral species and four *Millepora* species compared to 719 and 12 respectively in the Indo-west Pacific (de Weerdt, 1984; Mumby et al., 2014; Ruiz-Ramos, Weil, & Schizas, 2014; Spalding, Ravilious, & Green, 2001).

Fifteen scleractinian corals have been described in the brazilian coral reefs (C. B. Castro & Pires, 2001; Leão, Kikuchi, & Testa, 2003). These reefs also harbour four hydrocoral species of the Milleporidae family (Amaral, Steiner, Broadhurst, & Cairns, 2008; Ruiz-Ramos et al., 2014). In Northern Brazil, reefs are mostly fringing reefs with oceanic communities inhabiting these areas; the Abrolhos Reef is the southernmost true reef (18ºS), but coral assemblages have also been recordered at higher latitudes (23ºS) in Cape Frio (C. B. Castro & Pires, 2001).

The East Atlantic basin, also present some coral communities, such as those in Cape Verde (Monteiro et al., 2008; James D Reimer, Hirose, & Wirtz, 2010), Ascension Island (Bert W. Hoeksema, Nunes, Lindner, & De Souza, 2017; James Davis Reimer, Lorion, Irei, Hoeksema, & Wirtz, 2014) and the Canary Islands (Brito & Ocaña, 2004; Clemente et al., 2010). However, they are less diverse than those of the West Atlantic. The connectivity among these different Atlantic populations can provide insights into dispersal and evolutionary processes (Nunes, Norris, & Knowlton, 2011). Geological or natural enclaves (e.g. the Amazon estuary), currents (e.g the Gulf Stream, Fig. 5) and climatic conditions (e.g. temperature anomalies) mostly influence the dispersion/isolation of coral species acrros the Atlantic (Nunes et al., 2011).

Indo-Pacific coral reefs are the most diverse reefs on Earth. They encompass all types of reefs (atolls, barrier reefs, and fringing reefs) with more than 700 species of stony corals. They present major

biogeographic differences relative to the Caribbean reefs, with different trophic structure (Charles Birkeland, 1988), faunal composition (Sammarco, 1985), grazing pressure (C Birkeland, 1971), life-history traits (Charles Birkeland, 1988), habitat connectivity (Caspers, 1984), coral reproductive traits (Richmond & Hunter, 1990), species richness (Vermeij, 1978), and even ecological resilience (Connell, 1997), [reviewed in Roff & Mumby (2012)]. Apart from the high habitat diversity of this region (with many islands in close proximity); the Indo-Pacific is the centre of coral diversity due to the equatorial Pacific currents which act as traps for planula larvae by their direction of flow from west to centre (Fig. 5). Dispersal of corals (fragments and larvae) is passive: it is controlled by ocean currents and has a low probability of survival. For these reasons dispersion can highlight many aspects of corals biology (e.g. taxonomy and evolution) (Veron, 1985; Australian Institute of Marine Science AIMS, 2013).

The research presented in Chapter 2 is located in the Indian and Pacific Oceans, while the remaining investigations (chapters, 3, 4 and 5) are focus in the Atlantic Ocean (East and West Atlantic basins).

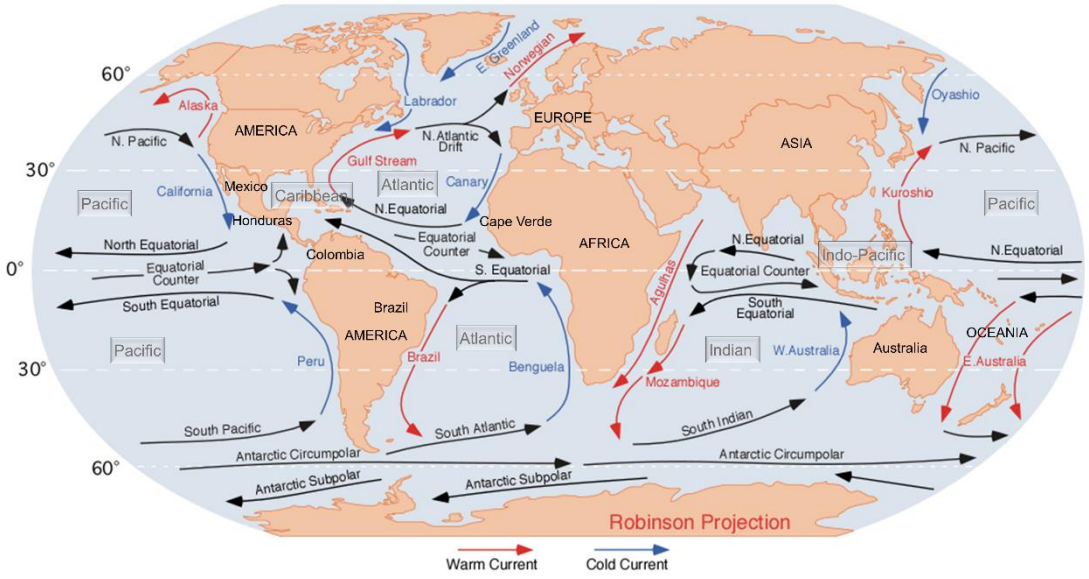

Fig. 5. Main ocean currents, from Dr. Michael Pidwirny (http://www.physicalgeography.net)

1.3.2. General methods: Correlative SDMs, Hybrid SDMs, Phylogenetic diversity indices, Genetic analyses

Corelative SDMs

The methodology used in three of the four main chapters of this thesis was the Species Distribution Models (SDMs) (**Chapters 2**, **3** and **4**). Correlative SDMs are statistical methods focused on the association between organisms' distributional records and geophysical, biotic and climatic factors (Anderson & Martínez-Meyer, 2004; Phillips, Anderson, & Schapire, 2006; Phillips, Avenue, & Park, 2004; Soberón & Nakamura, 2009). They estimate the habitat suitability, of one or more species, based on the correlation between presence records and environmental gradients (Guisan & Zimmermann, 2000) (Fig. 6).

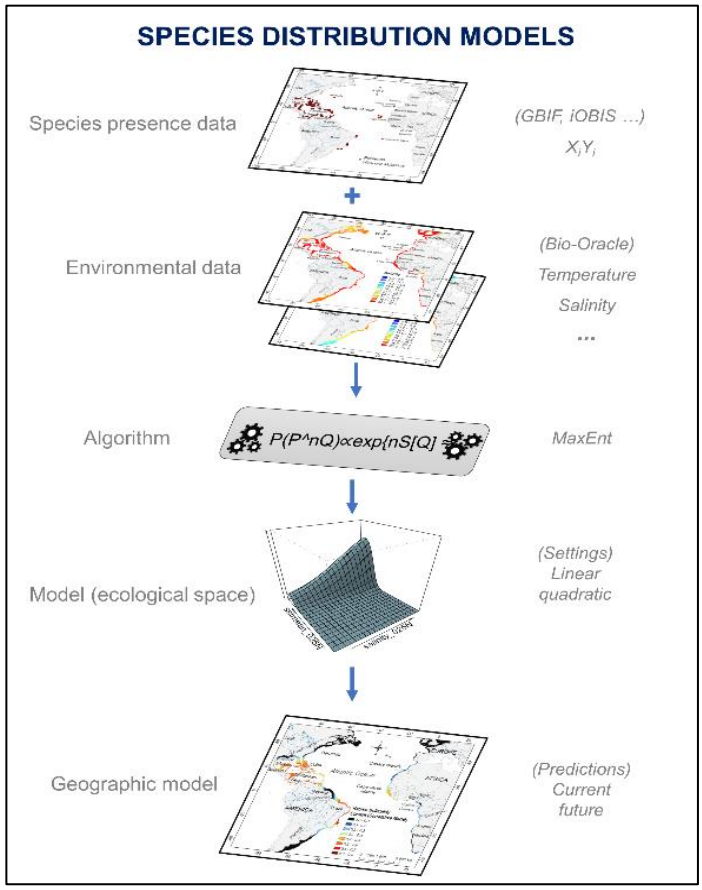

Fig. 6. General steps of a Species Distribution Model. The species presence records gathered from databases or field sampling along with the environmental variables are integrated in the SDM algorithm. The model settings are chosen, and geographical projections or future predictions are developed to estimate the habitat suitability of the species.

There are currenty more than 15 predictive SDM tools (Guisan & Thuiller, 2005), e.g. Bioclim based on the climate envelop (CE) method; Biomod which implements generalized linear models (GLM), generalized additive models (GAM), classification and regression trees (CART) and artificial neural networks (ANN); or MaxEnt based on maximum entropy (ME). From those, MaxEnt (Phillips & Dudík, 2008) is the most widely method used when only presence data is available (Elith et al., 2011). As mentioned above, MaxEnt is based on the Entropy theory, i.e, when all the elements of a dataset are equally likely, their entropy is maximum. Thus, MaxEnt tries to find the probability distribution which maximizes the entropy (uniform distribution), i.e. the most likely event; generating an output map of habitat suitability. In this thesis, several algorithms were analyzed, but MaxEnt was given preference due to its beter performance with presence-only data (commonly occurred in marine environments) compared to other methods; as well as, its extensive use in applied ecological studies by research organisations and government agencies (Porfirio et al., 2014).

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All these species distribution modelling methods, including MaxEnt, are based on the niche conception, which is the most variously defined and universally confused ecological concept (Real and Levin 1991). For example, Joseph Grinnel (1924)

described it as the "the ultimate distributional unit, within which each species is held by its structural and instinctive limitations" emphazising the abiotic (habitat) factors which influence where the species can be found (Grinnell 1917). The niche is a characteristic of the environment not the organism (Grinnel 1924; Martínez 2010). On the other side, Charles Elton (1927) defined the animal's niche as "its place in the biotic environment and its relations to food and enemies". It accentuates the function of a species within a food chain, while abiotic conditions are not relevant. And George Evelyn Hutchinson (Hutchinson 1957) explained the niche as "the hypervolume defined by the environmental dimensions within which that species can survive and reproduce". It is defined as a property of a species, not the environment (Pulliam 2000; Franklin and Miller 2010; Kearney et al. 2010). Hutchinson distinguished between the fundamental (potential or physiological) niche, as the response of species to environment (resources) without biotic interactions (competition, predation and facilitation); and the realized (ecological, actual) niche, as the dimensions of the environment in which species can be mantained (survive and reproduce), including biotic interactions (Austin and Smith 1989; Franklin and Miller 2010). These different interpretations have also influenced the terms used to discribe SDMs, e.g. 'species niche model', 'ecological niche model' or 'niche-theory model' (Franklin and Miller 2010); as well as the different niche estimation, e.g. the 'fundamental' or 'potential' niche, the 'realized' or actual niche, or, the 'climatic niche'. In this thesis the term SDMs is used for simplicity and generality, as in congruence with Franklin & Miller, (2010) for their accurate description of the modelling process and resulting model.

Some authors as (Austin 2002; Thuiller et al. 2004; Guisan and Thuiller 2005) [reviewed in Franklin and Miller (2010)] define the SDM as a realized niche, because models are generally based on current occurrences; so, it extrapolates in the geographical space those conditions associated with the species presences. Soberon and Peterson (2005) [reviewed in Franklin and Miller (2010)] state that SDMs based on large scales of climate variables, describe the fundamental niche. While Hirzel and Le Lay (2008) [reviewed in Franklin and Miller (2010)] identified that biotic interactions (competition and predation) tend to occur at short distances; and therefore, the fundamental and the

realized niche would be the same when predictions are made from large-scale environmental factors such as climate. Jiménez-Valverde et al. (2008) [reviewed in Franklin and Miller (2010)] suggest that when only presence data is used in SDMs, extrapolations are adequate, and the output represents the potential distribution (habitat suitability). However, when presence-absence data is used, interpolations are appropriate, and the prediction represents the realized distribution. The figure 7, extracted from Jiménez-Valverde et al. (2008), embodies the modelling techniques more appropriate for potential *vs* realized distributions; indicating that experiments and physiological data better describe the potential distribution, while complex methods with presence-absence data better represent the realized distribution.

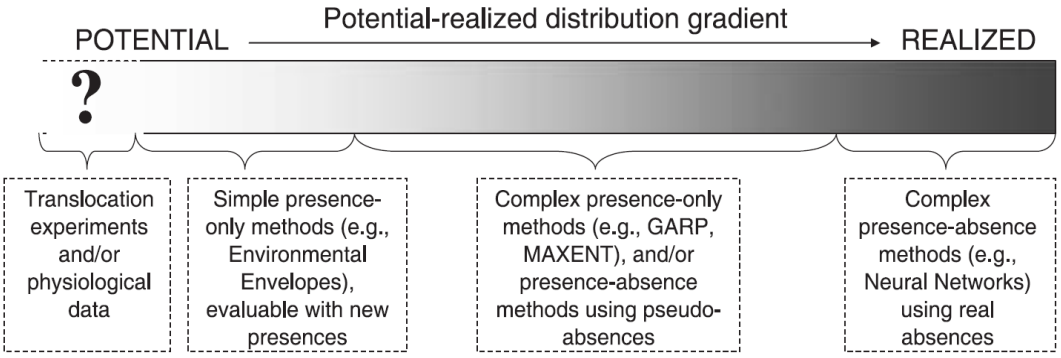

Fig. 7. A conceptual potential-realized distribution gradient showing the modelling techniques and the characteristics of the training (and evaluation) data that are more adequate to describe each portion of this gradient. Extracted from (Jiménez-Valverde et al. 2008).

These different interpretations of SDMs predictions, must be explicitly considered in each specific SDM study. Also, the equilibrium assumption of SDMs must be considered in these studies, which means that the species are expected to be in equilibrium with their environment, and that their observed distribution might represent the species' environmental tolerances, which is not usually the case for species that change their distributional ranges (Elith et al. 2010).

SDMs have been used to estimate geographic ranges in many marine organisms, for example, on fishes (Maravelias and Reid 1997; Wiley et al. 2003; Guinotte et al. 2006), seaweeds (Graham et al. 2007; Verbruggen et al.

2009; Martínez et al. 2012), jellyfish (Bentlage et al. 2009), crabs (Compton et al. 2010), cold-water corals (Davies et al. 2008; Tittensor et al. 2009), sponges (Knudby et al. 2013) and tropical corals (Tittensor et al. 2009; Bridge et al. 2012; Couce et al. 2012, 2013; Freeman et al. 2013). These are useful tools for making predictions of current and future species' potential habitats, which is crucial to evaluate species' probability of migration, extinction or invasion. Hence, they are used to support conservation plans and management policies (Guisan et al. 2013); e.g. planning new protected areas where the species extinction is high; or implementing control strategies to prevent species invasions (Thomas et al. 2004; Robinson et al. 2011; Marshall et al. 2014).

Hybrid SDMs

When projecting beyond the set of environmental factors used to train the model, correlative SDMs assume that the species physiological limits remain constant over space and time (Pearson and Dawson 2003; Monahan 2009). However, when the species response curve is trunkated in current conditions (i.e., physiological boundaries are not fully represented) and no physiologcal threshold is detected; extrapolations in space and time with more extreme conditions can be erroneously projected. For example, tropical corals currently live close to their upper thermal limits, but temperature increases (projected by climate change) can produce lethal consequences not detected by SDMs trained under current conditions. The incorporation of physiological knowledge, e.g. by mechanistic models, parameterized with physiological information (Monahan 2009; Kearney and Porter 2009), or by hybrid models, integrating correlative and physiological knowledge extracted from experiments (Buckley et al. 2010; Elith et al. 2010); can produce robust methods for extrapolating distributions to future environmental conditions, solving these constraints (Evans et al. 2015) (**Chapter 4**).

Phylogenetic diversity indices

The information provided by SDMs (habitat contraction or expansion) under different climatic scenarios (e.g. A2, B1, A1B of IPCC 2007) can detect new areas of potential extinction or invasion. When SDMs are applied to all the species within a region, future habitat changes can also inform about future changes in species richness and other diversity indices. Additionally, when phylogenies are incorporated into the analyses,

phylogenetic diversity indices can be detected and compared under current and future conditions (**Chapter 3**).

Some indices measure 'how much' biodiversity exists within assemblages; e.g. species richness, Faith's Phylogenetic Diversity (PD) or evolutionary distinctiveness (ED) (Tucker et al. 2017). Other indices test 'how different' the assemblages are; i.e. the divergence or phylogenetic relatedness among taxa. An example of these metrics are the standardized PD (PD_{SES}) or the Phylogenetic species variability (PSV) (Tucker et al. 2017). When current and future (potential presence/absence) information is available, the comparison of these indices provide potential changes of diversity patterns, which can be used to conform the base criteria for defining conservation areas (Brooks et al. 2002; Hickerson et al. 2010). Additionally, testing whether future habitat contractions predicted by SDMs is connected with phylogenetic clustering across species can reveal an important loss of evolutionary history, reflecting the vulnerability of certain lineages against climate change (Thuiller et al. 2011). The combination of SDMs along with phylogenetic analyses provides the information needed to guide and support conservation strategies to protect vulnerable communities facing climate change effects, as coral reefs.

Genetic analyses

As mentioned before, SDMs can detect new areas of potential extinction or invasion. The arrival of certain species into new regions can be produced via different pathways of dispersion. However, sometimes the pathway followed by the species is unknown, or the original source is uncertain. In these cases, the use of genetic analyses can help to elucidate the origin of new populations and support dispersal theories and strategies (**Chapter 5**). The use of molecular techniques has revolutionized our knowledge of molecular ecology and genomics (Patwardhan et al. 2014; Creer et al. 2016). Their use can be applied to describe diversity patterns within and between populations for inferencing ecological processes. The figure 8 represents the main general steps involved in studying molecular phylogeny using molecular markers (Patwardhan et al. 2014). The taxonomic level chosen for the study purposes is relevant for the consequent steps. The most often molecular markers used in genetic studies include nuclear ribosomal (rRNA) and the mitochondrial DNA (mtDNA) sequences (Patwardhan et al. 2014). The rRNA

(transcription of rDNA) harbours highly conserved as well as variable domains. The two subunits composing the ribosome, the small ribosomal subunit (SSU) and the large ribosomal subunit (LSU) can contain different rRNA species depending on which kingdom the organism belongs to. For example, in eukaryotes the SSU contains the 18S rRNA, and the LSU the 5S, 5.8S and 25S/28S rRNAs. In other domains, e.g. prokaryote (Bacteria and Archaea) the SSU contains the 16S rRNA and the LSU the 5S and 23S rRNA (Patwardhan et al. 2014). Since rRNA are genes that evolve more slowly compared to protein encoding genes, they are relevant in genetic analysis of distantly related species (Moritz, Dowling, & Brown, 1987; Patwardhan et al., 2014). On the contrary, the Internal Transcribed Spacers (ITS) of the nuclear rRNA have rapid evolution rates (Baldwin 1992), making them perfect for resolving phylogenies of closely related taxa. Regarding mitochondrial genes, they are usually very resolutive in species-level analyses. The enzymes Cytochrome oxidase I/II (COI/II) found in the mitochondria, evolve more slowly than other protein coding mitochondrial genes and have been used from species to population analyses. We can also find plastid (chloroplast) and mitochondrial ribosomes, so some fragments (e.g. 4S, 12S y 16S) can also be found in some of these organelles. All these gene fragments have been widely used in resolving phylogenetic analyses of corals and hydrocorals, and their endosymbionts (e.g. Santos et al. 2002; Meroz-Fine et al. 2003; Govindarajan et al. 2005).

There exist numerous toolkits or laboratory protocols for extracting DNA from plants and animals (e.g. Qiagen). The DNA is firstly extracted from tissue samples, then amplified and finally assembled. Thanks to the creation of public online databases, as GenBank (Benson et al. 2012), millions of nucleotide sequences are also available in just one click for scientific purposes. GenBank database provides a large source of genetic information ready to be included by scientists in their researches. Once all the sequences are obtained, they must be aligned for analyses purposes, for example using computer programs as MEGA: Molecular Evolutionary Genetic Analysis (Kumar et al. 2016). Then, the sequences can be compared to understand the evolutive relationships among organisms. Differences among sequences are indicative of genetic divergence (evolution), while similarities indicate genetic conservation across time

(Patwardhan et al. 2014). Phylogenetic trees are the most common graphical representation of these relationships, although other ways of representation, such as haplotype networks are also frequent. The construction of these graphics can differ among methods; e.g. Maximum Likelihood, Neighbour Joining, MrBayes, NeighborNet or Split Decomposition.

All these approaches can provide an integrative scientific vision on the ecology of corals under climate change.

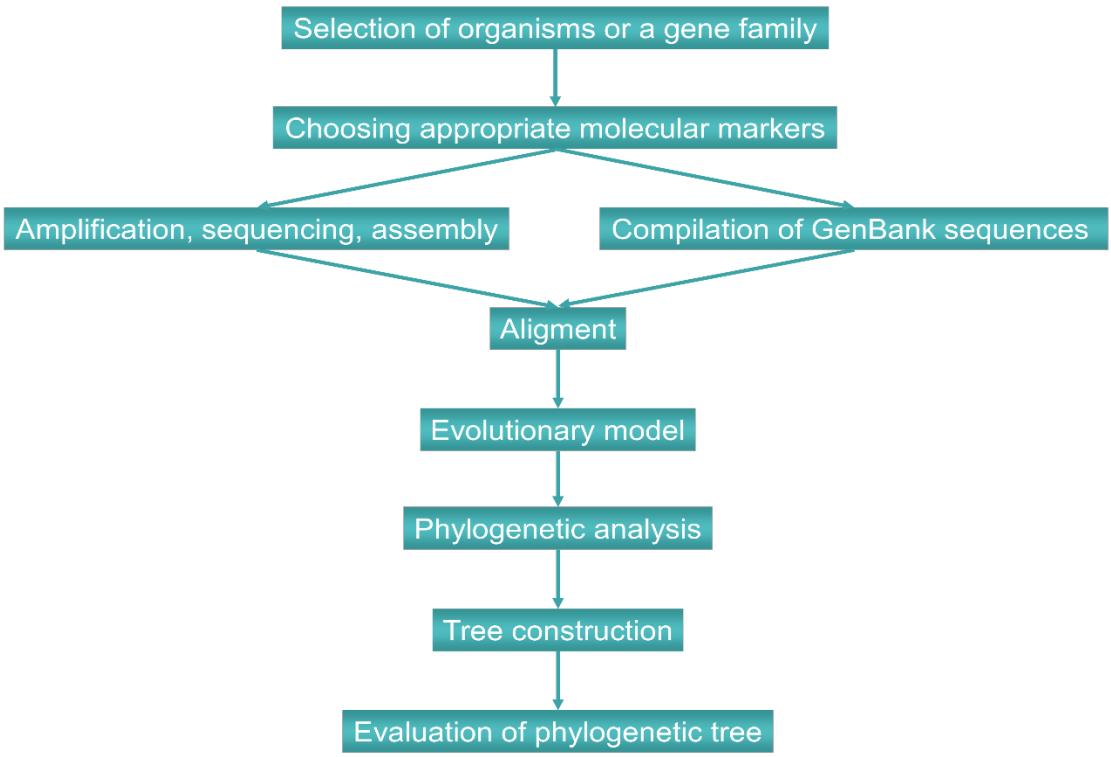

Fig. 8. General steps in studying molecular phylogeny, modified from Patwardhan et al. (2014).

1.4. Thesis Outline and Objectives

This thesis aims to contribute substantially to an integrative knowledge of the most relevant ecological responses of tropical corals undergoing climate change. In particular, the intention of this dissertation is to delve into **(1)** the potential distributional changes of tropical corals

(Scleractinia and Milleporidae) in future scenarios, as well as **(2)** into the possible pathways of dispersion and genetic relationships of expanding species. In addition, this thesis aims to **(3)** explore the potential future changes in the phylogenetic diversity of the communities that make up these reefs.

Some of the specifics goals of this thesis are:

1. To explore the future distribution of coral reefs under climate change.

2. To detect which coral species will contract or expand their ranges.

3. To detect the most critical areas to apply conservation strategies.

4. To detect future implications of coral species range contraction/expansions for the diversity of coral assemblages.

5. To detect future changes in the phylogenetic diversity of the Atlantic coral reef communities.

6. To develop a hybrid SDM that facilitates extrapolation into non-existent climates by including physiological information of the species.

7. To detect the dispersion and genetic relationships of a tropical hydrocoral and their symbionts between different locations across the Atlantic.

8. To explore the mechanisms of adaptation to the environment of corals' symbionts.

9. To develop tools and generate knowledge to optimize the conservation of tropical corals.

In accordance with these objectives, the core of this thesis has been structured as follows:

Chapter 2: ***Environmental factors driving the distribution of the tropical coral* Pavona varians*: predictions under a climate change scenario***.

This chapter explores which environmental variables most influence the distribution of *Pavona varians*, a hermatypic coral from the equatorial Indian and the Pacific Ocean, which is categorized as `Least Concern´ by the UICN and as `stress-tolerant´ coral by the functional classification of Darling et al. (2012). In this section, the future habitat suitability of *P. varians* is predicted under a current and a future intermediate IPCC scenario (A1B) using MaxEnt. The hypothesis of this chapter is that *P. varians* will decrease its current distributional

range under a climate change scenario because the temperature increases will be higher than the tolerance of the species, despite being an opportunistic species, with a well-known resistance to environmental stress.

This manuscript is currently under review in the journal *Marine Ecology*.

Chapter 3: ***Atlantic corals under climate change: modelling distribution shifts to predict richness, phylogenetic structure and diversity changes***

This chapter predicts future distributional changes of 45 Atlantic scleractinian corals under a climate change scenario. The binarization of the current and future (severe A2 IPCC scenario) habitat suitability predictions of the 45 coral species generates information regarding their potential presence/absence in each pixel (community) of the map. In this chapter it is also analysed whether these changes (expansions and contractions) are randomly distributed across the coral's phylogeny. Richness and different phylogenetic diversity indices (PD, PD_{SES} and PSV) associated with the Atlantic scleractinian reef communities are compared in current and future predicted conditions. This information is used to detect areas with evolutionary diversity losses, and hence of potential conservation interest. Additionally, this research identifies the most critical species to conserve due to their high evolutionary distinctiveness.

This manuscript is under review in the journal *Biodiversity and Conservation*.

Chapter 4: ***Integration of physiological knowledge into Hybrid Species Distribution Modelling to improve forecast of distributional shifts of tropical corals***

In this chapter, it is proposed a pioneer hybrid modelling method to forecast the potential distributional shifts of tropical corals facing global warming by integrating the physiological response function of the species to temperature as a novel physio-climatic predictor in a correlative SDM. A comparison of the results of the hybrid model with simple physiological and correlative SDMs is developed. The hypothesis of this research is that the hybrid model allows extrapolations in non-analogous conditions performing better and generating more realistic projections in geographic areas where future temperatures will exceed the species thermal limits, compared to other SDMs methods.

The results of this manuscript are published in the journal *Diversity and Distributions*. 2019; 00:1–14. doi.org/10.1111/ddi.12883

Chapter 5: *Genetic relationships of the hydrocoral* Millepora alcicornis *and its symbionts within and between locations across the Atlantic*

The fifth chapter addresses the genetic structure of the main Atlantic populations of the hydrocoral *Millepora alcicornis*. Multi-locus analysis, for both *M. alcicornis* and its associated symbionts, are used to disentangle the genetic relationships within and between their populations from both sides of the Atlantic, establishing the areas of origin of the recently established colonies in the Canary Islands and their associated symbionts. The hypothesis of this study is that the genetic origin of the Canarian colonies is the Caribbean region, as well as that of their associated symbionts. The results of this study will provide new insights into the ecological responses of these organisms to acclimate to the ongoing global warming.

This manuscript is published in the journal *Coral Reefs*. DOI: 10.1007/s00338-019-01772-1

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CHAPTER 2

Environmental factors driving the distribution of the tropical coral *Pavona varians*: predictions under a climate change scenario

Picture extracted from 'coral.aims.gov'

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Abstract

Climate change is affecting eco-physiological responses of a range of organisms, which may shift their geographical distribution boundaries. Modelling techniques predict the distribution of species by relating climatic and physical factors with species' presence records, including potential extinction areas and new potential areas of colonization under predicted climatic scenarios. In this study, we explored which environmental variables most influenced the distribution of Pavona varians, a hermatypic coral from the equatorial Indian and the Pacific Ocean, which is categorized as `Least Concern´ by the UICN. The most influential variables were the minimum and maximum sea surface temperature, the diffuse water attenuation and the cloud cover. These variables were used to predict habitat suitability of *P. varians* under a current and a future (A1B IPPC) scenario using MaxEnt. Despite P. varians is an opportunistic species, with a well-known resistance to environmental stress, the model predicted a massive decline in all areas by the year 2100. The information obtained by this study can be used to support the conservation decision making process to improve the preservation of the species.

Introduction

Climate change is impacting on living organisms of planet Earth, causing changes in their vital rates, phenology and physiological processes, such as changes on their growth, respiration, photosynthesis, and even advances or delays in their life cycle stages (L. Hughes, 2000). Climate change, particularly global warming, cause shifts in their geographical distributions, so species may reach new areas under favourable conditions (Parmesan et al., 1999), e.g. towards the poles or higher altitudes (González Elizondo et al., 2003; Walther et al., 2002), but may disappear from those areas under environmental stressful conditions (L. Hughes, 2000; Thomas, Franco, & Hill, 2006). Distributional shifts towards suitable areas are not possible in all species, since some of them have limited plasticity in their physiological tolerance, or restricted dispersion, driving local extinctions. The disappearance of habitat-forming and foundation species is particularly worrying, as it has been shown to cause the decline and collapse of the whole community (Wernberg, Russell, Thomsen, & Connell, 2014), favouring the increase of opportunistic and invasive species (González Elizondo et al., 2003;

Hoffmann & Sgró, 2011) with negative impacts on biodiversity (Ellison et al., 2005). The early detection of these potential changes, the environmental factors that most affect them, and the most affected areas, becomes a significant advantage when making conservation decisions (Guisan et al., 2013).

In the oceans, the most important effects of climate change are rising seawater temperatures, acidification resulting from increased CO_2 absorption, sea level rise, and changes in the global system of ocean currents (Gattuso, Hoegh-Guldberg, & Pörtner, 2014). The potential impacts of these environmental changes on organisms depend on whether they can tolerate and adapt to these effects. The distribution of marine ectotherms is closely linked to their thermal limits (Sunday, Bates, & Dulvy, 2012), so seawater temperature changes can trigger distributional shifts. Temperatures above the organism's tolerance threshold can also compromise their survival. Additionally, organisms subjected to temperature increases, near their sub-lethal thresholds, can also become more sensitive when faced with other of the aforementioned stress factors, such as acidification in corals (Prada et al., 2017).

Coral reefs are one of the most vulnerable and threatened marine ecosystems in the world. More than half of the world's reefs are at risk of degradation, and the vast majority has already disappeared (Burke, Reytar, Spalding, & Perry, 2011; P. Castro & Huber, 1997). Due to global warming, reef-forming species are currently shifting towards higher latitudes, at an approximate rate up to 10 km per year (Takao et al., 2015). However, other factors besides temperature also limit the distribution of corals at high latitudes, such as lowered pH, which generates a decay of the carbonate ions necessary for the formation of coral skeletons, or low light intensities that may concurrently limit the photosynthesis of the symbionts (Couce et al., 2012; Guan, Hohn, & Merico, 2015; Ove Hoegh-Guldberg, 2012; J.A Kleypas, McManus, & Meñez, 1999). In addition, local disturbances, such as eutrophication, sedimentation or overfishing, can also negatively affect the health of corals (Carpenter et al., 2008). The worldwide degradation and loss of coral reefs entails the loss of their associated ecosystem services, because, as foundation organisms, they provide shelter and food for marine fauna, coastal protection against wave erosion, as well as resources for the livelihood of about half a billion people

(Edwards & Gomez, 2007; G. P. Jones, McCormick, Srinivasan, & Eagle, 2004). Actions to mitigate climate change impacts are essential to ensure the viability of tropical reefs (Gattuso et al., 2014); the identification of areas where corals can be most affected by these environmental changes is key for adequate conservation plans. Within this context, only few studies have aimed to predict changes, under climate change scenarios, in the distribution of corals (Chefaoui, Casado-Amezúa, & Templado, 2017; Guinan, Brown, Dolan, & Grehan, 2009; Tittensor et al., 2009; Woodby, Carlile, & Hulbert, 2009), including tropical corals (Couce et al., 2013; E. C. Franklin, Jokiel, & Donahue, 2013; Freeman et al., 2013).

There are several modelling approaches for predicting the impacts of climate change on the geographic distribution of species (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000), but the most popular technique is the *Species Distribution Model* (SDM) (Elith et al., 2010). This modelling correlates the presence records of a species with environmental conditions to produce maps of projected habitat suitability, allowing extrapolations under future climate scenarios (Elith et al., 2010). Predictive modelling is a useful tool for supporting conservation decision making (Guisan et al., 2013). Modelling is especially relevant for species inhabiting habitats difficult to sample, as subtidal marine species, e.g. kelp forests (Franco et al., 2017; B. Martínez et al., 2012; Méléder, Populus, Guillaumont, Perrot, & Mouquet, 2010) and corals (Couce et al., 2013; E. C. Franklin et al., 2013; Freeman et al., 2013; Riul et al., 2013). One of the most common methods to relate the distribution of species with climate and other physical factors is the Maximum Entropy Model (MaxEnt) (Phillips et al., 2006). Compared to other statistical approaches, MaxEnt offers high predictive performance when species-absence data are unavailable (Jueterbock et al., 2013), as commonly occurs in the marine environment.

In this study, we focus on a scleractinian coral species, *Pavona varians*, whose geographic distribution extends over the tropics (excepting the Atlantic), being abundant across the eastern Pacific, as well as in islands from Costa Rica, Colombia and the Clipperton Atoll (Glynn & Ault, 2000; Glynn, Veron, & Wellington, 1996; H M Guzmán & Cortés, 1992; Hector M Guzmán & Cortés, 2001). Due to its strictly tropical distribution, it can be considered a potential species whose centre of distribution will likely decline, if the effects of climate change are maintained

according to the IPCC projections (Couce et al., 2013). However, this species is a stress-tolerant coral (Darling et al., 2012), which can cope with environmental stress and habitat loss, appearing in many regions where most corals are declining (Wilkinson, 2006); the species is categorized by the UICN as of "Least Concern". It is a broadcast spawner with a hermaphrodite mode of reproduction, showing increased spawning at high temperatures (Glynn, Colley, Ting, Maté, & Guzmán, 2000). These traits lead us to question if the habitat suitable of this species would decline by the negative effects of climate change, as generally predicted for coral reefs (Couce et al., 2013) or, alternatively, it would be maintained, withstanding the conditions of an intermediate IPCC scenario. This study has a dual aim: understanding the relative importance of environmental variables driving the current distribution of *P. varians* and predicting potential habitat shifts under a future intermediate climate scenario. Additionally, the results obtained can be used to support the conservation decision making process to improve the preservation of the species.

Material and methods

Distributional records

Scientific bibliography and three different databases were used to obtain presence records. The databases were: the *World Register of Marine Species* (WoRMS), the *Global Biodiversity Information Facility* (GBIF), and the *European Marine Observation Data Network* (EMODnet). These databases contained georeferenced information of the species records (last accessed, December 2014); when coordinates were not available, a description of the name of location was provided. In these cases, locations were searched with *Google Maps* and *Mapcarta* servers to find the exact points in which *P. varians* was registered. Duplicated records in distances <0.1º were discarded, resulting in 68 reliable coordinates out of 350 presences of *P. varians* around the Indian and Pacific.

Environmental variables

A total of 12 environmental variables, original raster resolution of 0.08º (~9.2 km^2), were downloaded from Bio-ORACLE (Table S1), a database of global predictors for marine species modelling (Tyberghein et al. 2012; http://www.oracle.ugent.be/, downloaded on March 2015). The layers were up-scaled to match the resolution of records (0.1º), using bilinear interpolation (Natale, Desoli,

Giusto, & Vernazza, 1993). Environmental variables were typified using several metrics, particularly the maximum and minimum, as they are directly linked with an organism' tolerance thresholds, computed from different time periods between 1997 and 2010. We here included: Sea Surface Temperature (SST), the concentration of Nitrate and Phosphate, Chlorophyll *a* (Chl*a*), Dissolved Oxygen (DissOx), ocean acidity (pH), Salinity, the percentage of Cloud cover (Cloud), the Available Photosynthetic Radiation (PAR), and the Diffuse attenuation at 490 mm(m^{-1}) of the water column (Da).

A GIS project implemented in ArcGIS 10.1 (ESRI, Redlands, CA, USA) was used to manage all spatial information. Environmental variables were restricted to depths < 100 m to exclude unsuitable seabed areas. To avoid autocorrelation between variables, a Spearman correlation matrix (Sokal & Rohlf, 1969) was obtained. When a pair of predictors were highly correlated, r_s > |0.85|, only the variable more causally related to coral biogeography was selected for subsequent analysis. The variables finally chosen for modelling were: maximum and minimum SST (SSTmax and SSTmin, respectively), Nitrate, Phosphate, Salinity, pH, maximum Cloud, PAR and Da (Cloudmax, Parmax and Damax, respectively). Multicollinearity through Variance Inflation Factor (VIF) was explored; all variables had VIF values <5 (Chatterjee & Hadi, 2015).

Species Distribution Modelling

We used the Maximum Entropy Modelling (MaxEnt, v. 3.3.3k, Phillips et al. 2006; Phillips and Dudík 2008) to explore the importance of variables defining habitat suitability of the species, discarding those with limited contribution. We aimed to develop a parsimonious reduced model for projecting the current and future habitat suitability of *P. varians*; models with few variables are preferred for explicative and predictive purposes (Austin 2002; Elith et al. 2010; Merow et al. 2014; Moreno-Amat et al. 2015). After exploring the model with different settings (Moreno-Amat et al. 2015), we chose that which better fitted the response curves of habitat suitability to environmental predictors. The model was constructed with linear, quadratic and hinge setting functions, which are recommendable to detect physiological tolerance thresholds (Merow et al. 2013; Moreno-Amat et al. 2015). The model was implemented with automatic regularization and β-multipliers (since models previously tested with high values oversimplified the

response of some variables), and a maximum number of iterations of 1,000.

MaxEnt shows the percent contribution of each variable to the model, i.e. the amount of variation provided by each variable. A permutation importance score is provided for each variable to denote its contribution. In addition, a coefficient of importance, calculated through a Jackknife randomization, estimates the predictive power lost every time a variable is left out from the model, while its contribution is assessed when it is the only variable considered (Phillips et al., 2006). The variables with a percent contribution and permutation importance < 10, and those of least importance according to Jackknife coefficients, were discarded when making projections. Additionally, we graphically explored the range of environmental conditions related to the presence records, by constructing histograms for each variable. These were compared with the response functions and the habitat suitability map projected by MaxEnt under current conditions.

Projections

Only the most important variables selected by MaxEnt were included in a reduced model to predict the habitat suitability of *P. varians* under current and future conditions. The layers containing future environmental conditions of maximum and minimum sea surface temperature were downloaded from Bio-ORACLE, specifically for the A1B scenario for the year 2100 (Nakicenovic et al., 2000). This scenario considers an intermediate level of pollution, with a global CO_2 emission of 750 ppm from energy and industry (IPCC, 2000), and temperatures between 1.7 and 4.4°C higher relative to nowadays (Meehl et al., 2007). 2007). These layers were rescaled and constrained to the coastline, following the aforementioned protocol, and then incorporated in MaxEnt to create a projected map of habitat suitability for 2100. As environmental projected layers were only available for SSTmin and SSTmax, we selected current conditions for the other variables. Finally, projections from the current and future climatic scenarios were compared to detect potential habitat expansions and contractions.

Validation

To quantify the performance of the models, we used the value of the area under the curve (AUC), operated by the Receiver Operating Characteristic curve (ROC) (Phillips et al., 2006). An internal partition of the data was applied in which 70% of the

data were randomly selected for training and 30% for testing; this procedure was repeated 10 times. Models with mean AUC values greater than 0.85 indicate good discrimination between suitable and unsuitable areas (M. Araújo, Pearson, Thuiller, & Erhard, 2005; Swets, 1988).

Results

Presence records

We gathered 68 reliable sites of current presence of *P. varians*, distributed by the equatorial zones of the Pacific and Indian Ocean (Fig. 1a), which corresponded to that previously described areas (Glynn & Ault, 2000; Glynn et al., 1996; H M Guzmán & Cortés, 1992; Hector M Guzmán & Cortés, 2001; B.W. Hoeksema, Rogers, & Quibilan, 2014). The species is distributed across Pacific archipelagos and atolls, such as Papua New Guinea, Guam, Northern Mariana Islands, Kiribati and Marshall Islands (Micronesia), Fiji, Cook Islands, French Polynesia, Hawaii and Pitcairn Islands. Closer to the American continent, it is found in Galapagos (Ecuador), Isla Uva (Panamá) and Isla Gorgona (Colombia). In the Indian, it appears in Seychelles, Maldives and Coco Islands. Between the Indian and Pacific Ocean, *P. varians* is extended from Singapore to South of Japan (Okinawa), Papua New Guinea, northern Australia and New Caledonia; the largest amount of presences is found in Indonesia. The northern latitudinal boundary is found on Midway Island (Hawaii, 28°13' N); the southern latitudinal boundary is found on Henderson Island (Pitcairn Islands, 24°22' S), both in the Pacific.

Selection of predictive variables

The full model was trained with the nine variables previously selected. After running this model with MaxEnt, a set of variables that significantly contributed to explain the geographic distribution of the species with a % contribution, or permutation importance > 10 (Table 1a), were selected for a final predictive model (Table 1b). SSTmin had the greatest explanatory power, followed by Damax, Cloudmax and SSTmax. The five remaining variables (Parmax, Nitrate, Phosphate, pH and Salinity), whose contribution was minor, were, therefore, discarded. These results were congruent with the Jackknife's test (Fig. S1), showing that Damax was the variable that contributed with the highest gain (0.22), while SSTmin was the variable that most decreased the predictive power of the model when omitted.

Table 1 Relative contributions of environmental variables to the MaxEnt model. (a) Full model with all non-correlated variables. Variables with a percentage < 10% (in grey) were discarded to produce the (b) reduced model.

a)	**Full model**	
Environmental variable	Percent contribution	Permutation importance
SSTmin	26.1	42
Damax	19.5	12.2
Cloudmax	16.4	5.8
SSTmax	13.6	17.2
Parmax	7.6	3.3
Nitrate	4.8	3.5
Phosphate	4.5	4.3
pH	3.8	3.2
Salinity	3.7	8.5
b)	**Reduced model**	
Environmental variable	Percent contribution	Permutation importance
SSTmin	41.5	56.2
SSTmax	23.3	25.5
Damax	19.2	4.8
Cloudmax	16	13.8

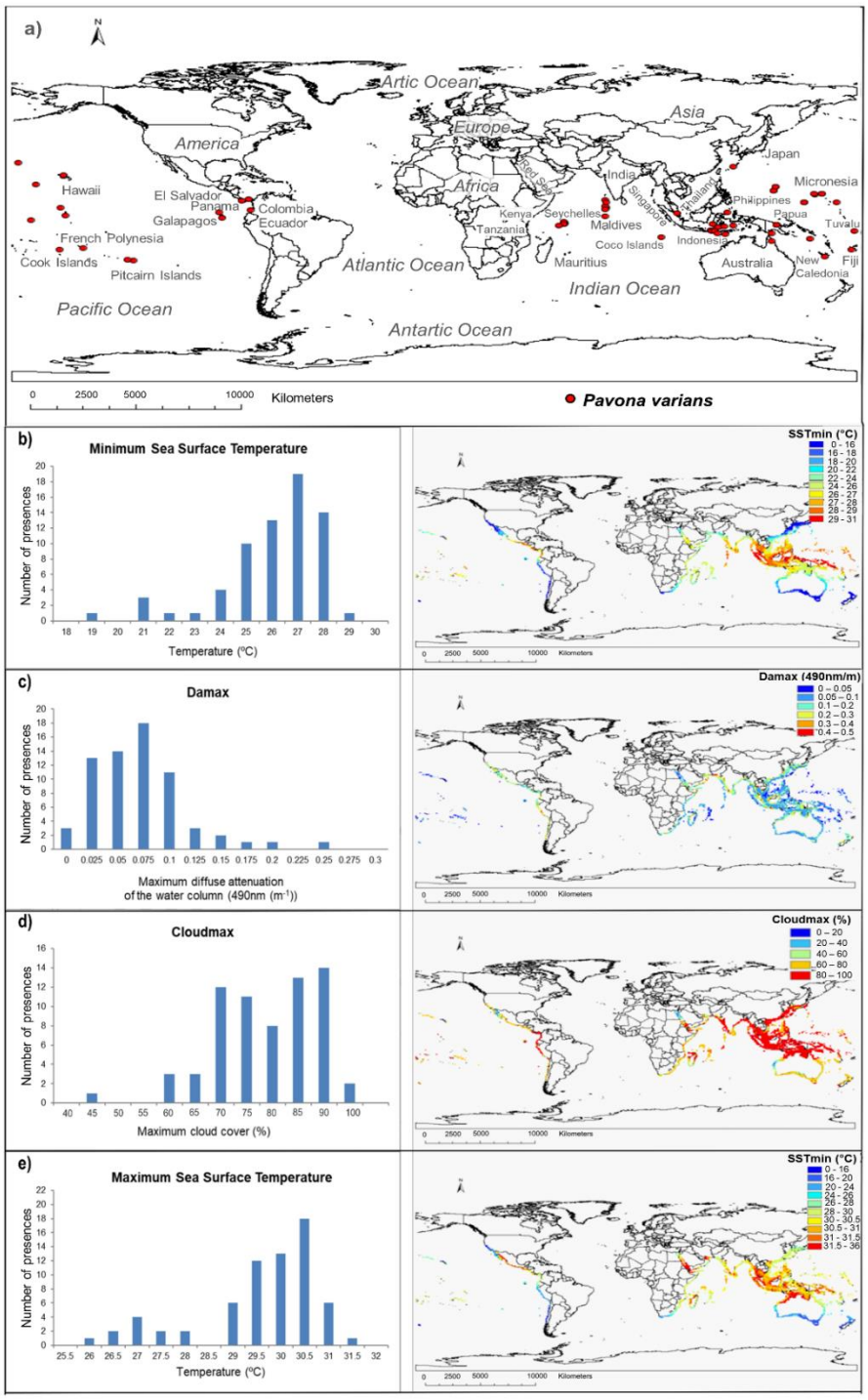

Fig. 1 (a) World map with the presence records of the coral *Pavona varians*. (b) Minimum sea surface temperature (SSTmin), (c) maximum diffuse attenuation of the water column (Damax), (d) maximum cloud cover (Cloudmax) and (f) maximum sea surface temperature (SSTmax). Left: Histograms with the frequency of *P. varians* in relation to environmental ranges. Right: Gradient map with the values of each environmental variable.

Habitat suitability at current conditions

According to the histogram relating coral presences with SSTmin values (Fig. 1b-left), the minimum SST with occurrences of *P. varians* ranged between 19°C and 29°C, with the highest frequency between 25°C and 28°C. The latter range corresponded to the Indian and Pacific islands (e.g. Mauritius, Maldives, Philippines and Micronesia). Preference for lower SSTmin values occurred only at high latitudes in the Pacific, e.g. Hawaii and Japan (ranging from 20ºC to 22ºC), and close to the equator in Galápagos (between 16ºC and 22ºC), due to the cold current of Humboldt, which causes lower temperatures than those expected for this latitude. Minimum temperatures > 28ºC showed a marked decrease in the species' presence (Fig. 1b-left), i.e. just one occurrence (Tuvalu) corresponding to 29ºC and none above this temperature.

According to projections of habitat suitability under current climatic conditions, high suitability values were estimated for coasts from the middle western America (e.g. Panama and El Salvador) and for islands and peninsulas from low latitudes in the Indian (e.g. Mauritius, Maldives and Thailand) and the Pacific (e.g. Philippines and Micronesia) (Fig. 2a). The exception was the coasts from Ecuador and Galapagos, due to the regional effect of the cold Humboldt current (Fig. 2a).

By large, SSTmin marked the latitudinal distribution limits of *P. varians*, being the variable with the highest importance in the SDM (Table 1b). However, habitat suitability varied within tropical regions because of the influence other variables. In terms of maximum sea surface temperatures, *P. varians* appeared in cells with temperatures up to 31.5 °C; the most favourable temperatures ranged from 28°C to 30.5°C (Fig. 1e-left). These temperatures appeared in oceanic regions close to the equator, such as central America, India, Indonesia and the Philippines ("Coral Triangle"), north-eastern Australia and Micronesia. Extremely warm temperatures, >31.5ºC, were not adequate for the coral, showing low suitability, e.g. in northern Australia and the Red Sea. Despite SSTmax did not limit the northern and southern latitudes in the distribution of *P. varians*, this variable limited the coral distribution in certain areas of high temperatures. For this reason, it was the variable with the second % of contribution in the SDM (Table 1b).

Within the latitudes bounded by SSTmin and areas with no lethal temperatures marked by SSTmax, the coral showed a preference for areas with low diffuse attenuation, up to a maximum of 0.25 nm/m (Fig. 1c-left). The lowest values of Damax (< 0.1nm/m) were found in small islands, where the occurrence of the coral was high (Fig. 1c-left-right). Values of diffuse attenuation > 0.25 nm/m were found in continental coasts (Fig. 1c-right), where projected habitat suitability was low, with the exception of certain eastern African coasts (e.g. Kenya) and central America (e.g. Ecuador), which have Damax values between 0.1 and 0.2 and habitat suitability > 0.5. Larger islands, such as those between the Indian and Pacific Oceans, also had high diffuse attenuation values, as do continents, and so their habitat suitability was also low (> 0.25) (Fig. 2a). Damax was the third variable with the greatest capacity to explain the distribution of *P. varians* (Table 1b), explaining differences of habitat suitability between islands and continental coasts.

Presences of *P. varians* appeared under cloud covers > 45% (Fig. 1d-left); the highest frequencies were found under cloud covers between 70 to 90%. Much of the areas with a cloud cover > 70% appeared in the tropical continental coasts and islands (Fig. 1d-right), coinciding with the Intertropical Convergence Zone (ITCZ). Current habitat suitability values > 0.5 were always found under a cloud cover > 40% (Fig. 2a). Therefore, the variable Cloudmax had an explanatory importance on the distribution of *P. varians*.

Model validation and future habitat suitability

The model showed an excellent performance, i.e. mean AUC value = 0.925. All the presence records appeared in areas of high suitability (Figs. 1a, 2a); the response curves of the SDM (Fig. S2) showed similar patterns relative to those of the histograms (indicating the environmental ranges where the species was present, Fig. 1).

According to future projections, a general and acute decrease of habitat suitability of *P. varians* was predicted by the year 2100. All regions had habitat suitability values very low, from 0 to 0.25, indicating major unsuitability for *P. varians* (Fig. 2b).

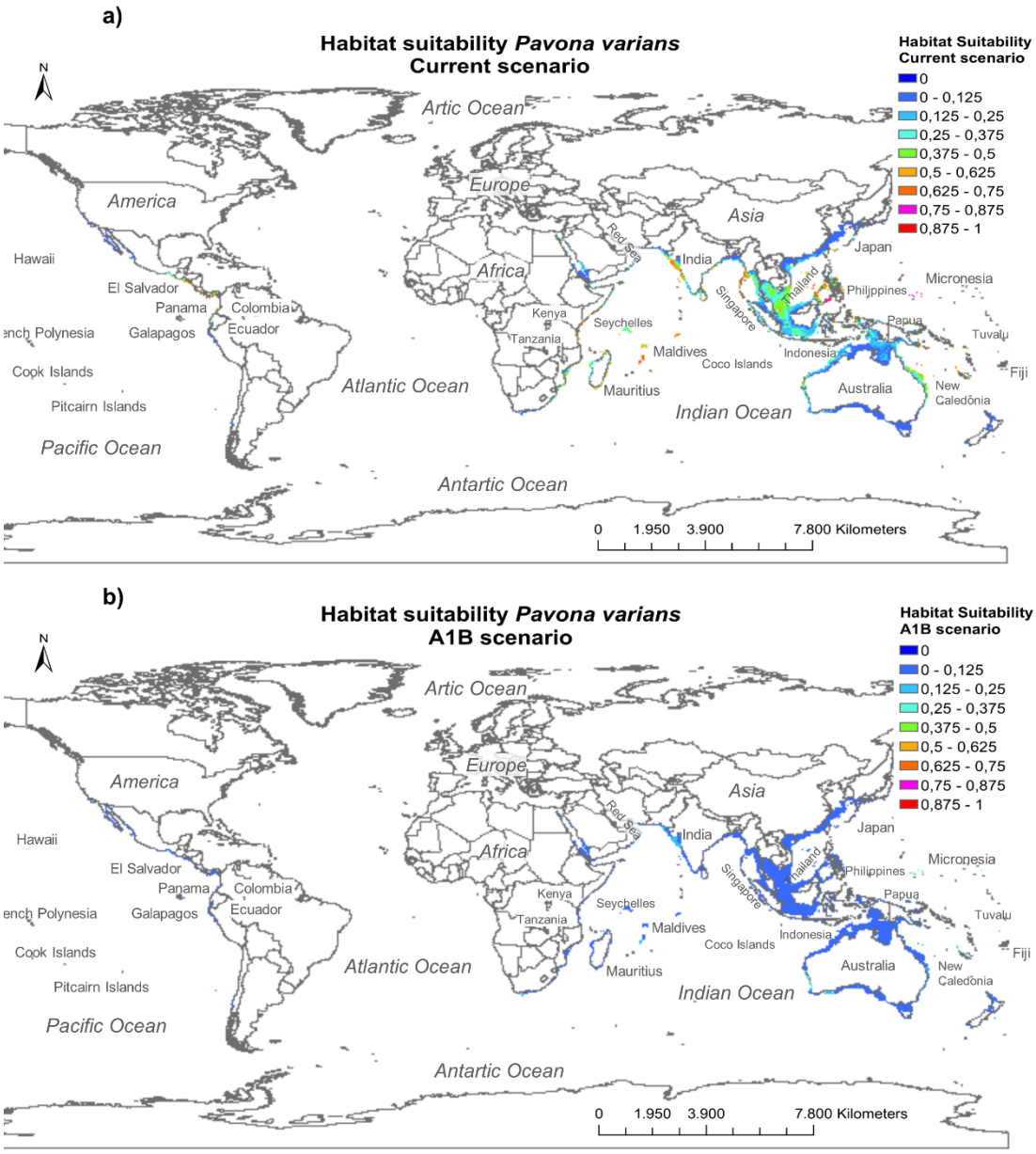

Fig. 2 Habitat suitability maps of *Pavona varians* under (a) current conditions and (b) future A1B IPCC scenario for the year 2100

Discussion

Detection and understanding of the main variables driving the global distribution of a specific coral can guide and reduce efforts of habitat conservation managers by focusing them on the most relevant variables. The main predictors can be considered first when managing strategic

conservation plans at global scales, leaving other potential impact factors for secondary local steps. Additionally, the prediction of the species habitat suitability can also help to prioritise their most vulnerable areas (Marshall, Glegg, & Howell, 2014). Among the set of variables considered in this study, the minimum sea surface temperature was the variable that best explained the current distribution of *P. varians* in tropical latitudes. The results also suggested the importance of the maximum sea surface temperature, showing a thermal threshold at 31.5ºC where the coral does not appear, most likely, because the seawater temperature is too high for its survival. Other variables, such as the maximum cloud coverage and the coefficient of diffuse water attenuation, were also important in determining the habitat suitable for *P. varians*. In summary, the best suitable areas were those with minimum sea surface temperatures from 24 to 29ºC and maximum sea surface temperatures from 28 to 30.5°C. Such areas mostly occur in equatorial zones, also characterized by low diffuse water attenuation and high cloud cover, except in areas of high runoff that promoted increased light attenuation. Nutrients, pH, diffuse attenuation and salinity were not relevant factors in the SDM because its variability did not highly affect the species distribution, or their local effects were masked by the global effects of the other variables here selected. Thus, they should be tackled in second place, in more specific local approaches.

The minimum seawater temperature marked the northern and southern limits in the distribution of *P. varians* across the Pacific and Indian Ocean. An exception was the southern limit in south America, near the Ecuador (equatorial region), as a result of the upwelling of cold waters associated with the Humboldt current (Humboldt, n.d.). Suitable temperatures for corals usually range between 20°C and 30°C (Badenas & Aurell, 1999; Nybakken & Bertness, 2001), with the best range between 25° and 29°C (Kinsman, 1964). These temperatures closely coincided with those accounted by the histograms of this study, since *P. varians* showed presence in cells between 19°C (SSTmin) and 31.5°C (SSTmax), with high frequencies between 24° and 29°C for SSTmin. The minimum temperature limit (19°C) of *P. varians* is common within hermatypic corals, because they contain symbiotic organisms (zooxanthellae) that require warm temperatures. The cold temperature intolerance of the coral is dependent on the cold photosynthetic tolerance of the

zooxanthellae; when seawater temperature declines, the photosynthetic potential of the zooxanthellae also decreases, reducing the fitness of the holobiont (Thornhill, Kemp, Bruns, Fitt, & Schmidt, 2008). A study by Suwa et al. (2008) applied to species of the genus *Pavona* (*P. divaricata* and *P. decussata*) showed that low temperatures (<18ºC) decreased the photosynthetic yield of their symbionts, which explains the limitation of the minimum temperature in the distribution of corals.

As most corals, *P. varians* requires clear waters (P. Castro & Huber, 1997; Ceh et al., 2013; Nybakken & Bertness, 2001). Waters with a low diffuse attenuation (<0.25) is typical of zooxantheallae corals, as sunlight can penetrate easily into the water column, providing sufficient light to carry out the photosynthesis (P. Castro & Huber, 1997; Lesser, Slattery, & Leichter, 2009; Nybakken & Bertness, 2001). Continental coasts generally have more land erosion and pollution than archipelagos, what is associated with turbid waters, via terrestrial runoff (Fabricius, 2005). This could have contributed to the low habitat suitability of these regions, as predicted by the current SDM. Only small continental coasts, e.g. Kenya, in Africa, and Ecuador, in central America, had low diffuse attenuation and, consequently, high suitability values, coinciding with areas of low human impacts (Halpern et al., 2008), including low plastic pollution (Eriksen et al., 2014).

According to our study, *P. varians* lives in regions with a high percentage of cloud cover, ranging from 70 to 90%. Tropical regions, typically within the ITCZ, commonly have a monsoon climate, including a wet season with abundant rain, and a dry season with less rain. Although corals need sunlight, clouds can provide protection from extremely hot temperatures. In this sense, endosymbionts residing inside zooxanthellate corals, as occurred with *P. varians*, can emit dimethyl sulfide (DMS), which is released into the atmosphere, facilitating cloud condensation (Charlson, Lovelock, Andreae, & Warren, 1987; Fischer & Jones, 2012; G. B. Jones & Trevena, 2005; Leahy, Kingsford, & Steinberg, 2013; Swan, Jones, & Deschaseaux, 2012). The ability to release DMS, and produce cloud cover above reefs, is a mechanism to regulate environmental conditions, maintaining the maximum seawater surface temperature below 30°C. This mechanism protects corals from possible water temperature anomalies and buffer strong solar radiation leading to reef whitening (Joan A Kleypas, Danabasoglu, & Lough,

2008; Leahy et al., 2013; Swan et al., 2012; Thompson & van Woesik, 2009).

The coral *P. varians* is a stress-tolerant species (Darling et al., 2012), behaving as a robust and opportunistic species under environmental stress (Wilkinson, 2006), being the first to colonize denuded areas (H M Guzmán & Cortés, 1992; Hector M Guzmán & Cortés, 2001). This species is expected to acclimatise better to global warming than their branched counterparts (Loya et al., 2001). For example, *P. varians* recruitment success was favoured by positive sea surface temperature anomalies, ranging from 0.5 to 1.5ºC, at Uva Island (Panamá) (Glynn et al. 2000). According to Glynn et al. (2000), densities of *Pavona* in the eastern Pacific declined after the strong Southern Oscillation of El Niño (ENSO) in 1982 and 1983; ten years later, the number of colonies in Caño Island (Costa Rica) and Uva Isla (Panama) were re-established to pre-ENSO levels. In addition, Sheppard et al. (2008) detected a marked increase in the cover of juvenile colonies of *P. varians* in 2006, after a high mortality event caused by a period of extreme temperatures in 1998 in Chagos. This archipelago, located in the centre of the Indian Ocean, coincides with an area, in which the current habitat suitability map showed high probability of favourable conditions. Initially, this body of research suggests this species may colonize new territories, while coping with climate change, as already suggested for other species, e.g. *Acropora spp.* (Takao et al., 2015). However, Glynn et al. (2000) also detected a limit in recruitment when monthly maximum SST anomalies exceeded 1.6ºC. Moreover, van Woesik et al. (2004) demonstrated that *P. varians* showed no bleaching after anomalous high temperatures in 1998, but it was less resistant after the high temperatures of 2001. The absence of *P. varians* under temperatures > 31.5ºC (e.g. northern Australia), along with the massive decline in almost all equatorial and tropical regions predicted by our future SDM, is consistent with those results. This outcome coincides with Couce et al. (2013), stressing future declines in the habitat suitable for coral reefs in tropical latitudes, due to seawater temperature increases. As a result, the initial ability of *P. varians* to withstand environmental stress may not be enough to persist under extremely high temperatures. The maximum thermal tolerance of the species, according to the response curves of this study, is at 31.5ºC (habitat suitability <0.3), which will occur across most of the entire study region by 2100 (Fig. S3), likely causing a general loss in the suitable

habitat. Those regions with temperatures <31.5ºC (e.g. southern Australia) would not be suitable, due to restrictive values of other relevant factors driving *P. varians* distribution (i.e., damax and cloudmax). Obviously, the incorporation of other sources of information, e.g. coral's physiological and genetic adaptation, dispersal and species interactions, or the effects of local anthropogenic disturbances, would improve the reliability of SDMs projections (Donner, 2009; Singer, Schweiger, Kühn, & Johst, 2018).

This study has demonstrated that the main climatic variable determining the global distribution of *P. varians* was the minimum sea surface temperature. Other relevant variables contributing to explain the distribution of *P. varians* were diffuse water attenuation, cloud cover and maximum sea surface temperature. Despite being considered a stress tolerant coral, our future SDM predicts an evident decrease in the habitat suitable for this coral, coinciding with global ocean warming. This research provides relevant information to support further management decisions to conserve the species in the future decades.

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CHAPTER 3

Atlantic corals under climate change: modelling distribution shifts to predict richness, phylogenetic structure and diversity changes

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Abstract

Climate change is altering species distributions worldwide. Particularly, global warming is driving range contractions and expansions of tropical species, such as corals. The use of climatic projections, via Species Distribution Models (SDMs) to predict species distributional shifts, can identify threaten species and help to set priority areas of conservation. These distributional changes might not be randomly distributed across the phylogenetic tree, so future extinctions may produce a disproportionately decline in their phylogenetic diversity, impacting regions with unique lineages. In this study, we assessed if distributional shifts (contractions/expansions) of 45 Atlantic reef-forming corals (scleractinian), and the main environmental variables driving their distributions, correlated with their phylogeny, i.e. whether expected contractions and expansions affected specific clades or not. We also estimated the potential loss and/or gain of species richness and phylogenetic diversity (PD), as well as implications in terms of the phylogenetic structure of communities (phylogenetic clustering, overdispersion or randomness), under future climate scenarios (year 2100, A2 IPCC) across the Atlantic. The potential loss of Atlantic corals in the future will be randomly distributed across their phylogeny, i.e. potential extinctions will not only affect one section of the phylogeny, therefore alleviating an inordinate loss of evolutionary history. Nearly all current and future communities present a random phylogenetic structure. Environmental variables did not show a significant correlation with the phylogeny. Predicted changes in species Richness, PD and Phylogenetic Species Variability (PSV) vary across the Atlantic; certain areas display large evolutionary diversity losses, highlighting their conservation relevance. Species belonging to isolated clades (high evolutionary distinctiveness) contribute to quantitative increases, or decreases, of PD and PSV, becoming crucial species for conservation. These findings highlight the importance of combining SDMs and phylogenetic metrics to develop conservation strategies to protect the future of coral reefs.

Introduction

Ongoing environmental changes observed in the last decades, such as global temperature rises, glacial retreats, and ocean acidification, are drastically impacting on biotic systems worldwide (IPCC, 2007; Walther et al., 2002). In

particular, global warming alters organisms' phenology, e.g. plants flower in advanced periods (Menzel et al., 2006). Concurrently, warming temperatures constrains animals' physiology, including reductions in growth and reproduction. Warming may also cause high mortality when temperatures exceed organisms' physiological thermal tolerance thresholds (García-Robledo, Kuprewicz, Staines, Erwin, & Kress, 2016; L. Hughes, 2000; Parmesan, 2006). As a result, species distributional shifts are rapidly occurring all over the world (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Elith et al., 2010; Hampe & Petit, 2005; Parmesan, 2006; Wernberg et al., 2016), often entailing catastrophic changes for local communities, including species diversity losses. For example, some fishes (Cheung et al., 2009; Fodrie, Heck, Powers, Graham, & Robinson, 2010; Heck, Fodrie, Madsen, Baillie, & Byron, 2015; Vergés et al., 2014) and birds (Wu & Zhang, 2015) are expanding their ranges to high latitudes. On the other hand, certain lizards and frogs are being constrained to isolated regions, or even becoming extinct because they cannot reach new areas under favourable environmental conditions (Sinervo et al., 2010; Thomas et al., 2006). Several species, such as certain butterflies, plants and tropical corals are experiencing both situations, i.e. range contractions in their areas of origin, but expanding their range to upper elevations or higher latitudes (Beaumont & Hughes, 2002; Feeley, 2012; Parmesan et al., 1999; Precht & Aronson, 2004; Thomas et al., 2006; R. J. Wilson et al., 2005).

Habitat contractions and expansions can be used as an index of species vulnerability to climate change (Carvalho, Brito, & Crespo, 2010; Guisan & Thuiller, 2005); this is also used as a criterion for classifying the conservation status of a species in the IUCN (International Union for Conservation of Nature). These habitat shifts can be predicted by applying Species Distribution Models (SDMs), which estimate the habitat suitability of a species based on the correlation between presence records and environmental gradients (Guisan & Zimmermann, 2000). Insight provided by the prediction of species' range shifts (i.e. contraction/expansion) can address diverse phylogenetic questions (Buckley & Kingsolver, 2012; Wilfried Thuiller et al., 2011). For example, the predicted extinction of a species from a community/ assemblage can dwindle the taxonomical and the Phylogenetic Diversity (PD) of such community/ assemblage. Aside from richness and

taxonomical diversity, measures of PD are widely used to set conservation priorities (Pollock et al., 2015; M. Winter, Devictor, & Schweiger, 2013) with the aim of minimizing the loss of evolutionary diversity (Tucker et al., 2017; Vane-Wright, Humphries, & Williams, 1991). There is a range of indices to account for different aspects of PD (Tucker et al., 2017); for example, the paramount Faith's (1992) index of PD is defined as the total branch length spanned by the tree, including all species in a local community. This measure depends on the size of the set of species (richness-dependant). However, other metrics of PD are invariant to species richness, such as the PD_{SES} (Standardized Effect Size) (Webb, Ackerly, & Kembel, 2008), or the phylogenetic species variability index (PSV) (Helmus, Savage, Diebel, Maxted, & Ives, 2007). The PD_{SES} is used to analyse the phylogenetic structure of a community. When closely related species, belonging to few lineages-clades-taxa, dominate, the community is phylogenetically clustered; the opposite, i.e. a phylogenetically overdispersed community denote a lack of phylogenetic structure. The (PSV) explains how diversity is structured, estimating the degree of phylogenetic relatedness (or evolutionary redundancy). The amount of PD lost in a community by the disappearance of a species varies depending on its phylogenetic relationships with their community relatives. Importantly, if the losses of species caused by climate change are not randomly distributed across the phylogeny, they can lead to a disproportionate loss of evolutionary history (Heard & Mooers, 2000; Nee & May, 1997; Wilfried Thuiller et al., 2011).

The information extracted from SDMs, in terms of the appearance/disappearance of species, along with phylogenetic analyses, can be useful for conservation purposes (Buerki et al., 2015). Thuiller et al. (2011) tested whether certain clades are more vulnerable to climate change than others using mega-phylogenies and predicted geographic changes/range shifts in plants, birds and mammals' suitable areas under different climatic scenarios. They forecasted that the vulnerability of species is weakly clustered across phylogenies, and that future phylogenetic diversity will decrease in southern Europe and increase at higher latitudes and altitudes. Detecting phylogenetic patterns, in particular the prevalence of phylogenetic clustering or overdispersion, i.e. whether co-occurring species are more or less closely related than expected by chance, has been widely

explored in the scientific literature for decades (Eldredge & Cracraft, 1980). If future habitat contractions are connected with phylogenetic clustering across species, i.e., taxonomically similar species share similar values of range contraction, this could represent an important loss of evolutionary history, reflecting the vulnerability of certain lineages under climate change scenarios (Wilfried Thuiller et al., 2011). This could be expected, since upper thermal physiological tolerances of species (which are one of the principal factors driving species range contractions) tend to be more similar in closely related species than in distantly related species (M. B. Araújo et al., 2013; Hoffmann, Chown, & Clusella-Trullas, 2013). Therefore, species may show a non-random pattern of range contractions across phylogenies. However, this is not so evident (Comte, Murienne, & Grenouillet, 2014); if no phylogenetic clustering pattern is detected, and random or phylogenetic overdispersion is shown, contractions may affect species indistinctly of their phylogenic similarities.

One of the most vulnerable ecological systems affected by climate change are coral reefs (O Hoegh-Guldberg et al., 2007; Parmesan, 2006). They are one of the most diverse and productive marine ecosystems in the world (Buddemeier et al., 2004; Ove Hoegh-Guldberg, 1999); consequently, any impact on their foundational species (corals and hydrocorals) could lead to a large-scale loss of global biodiversity (Carpenter et al., 2008). Corals have being part of our oceans over the last 250 million years (Ove Hoegh-Guldberg, 1999), and they are among the most long-lived species on the planet (Kaplan, 2009). The global distribution of corals has varied slowly through geological time (Buzas & Culver, 1994; Wood, 1998), but recent environmental changes are causing an unusual and accelerated modification of their distribution patterns (O Hoegh-Guldberg et al., 2007; Precht & Aronson, 2004). In particular, corals are being excluded from places under extreme hot temperatures, e.g. in some parts of the Great Barrier Reef by massive bleaching events (L. Hughes et al., 2016), but they are also expanding their range to warming latitudes (Yamano et al., 2011). Climate projections can be used to detect the future magnitude of these potential changes in corals (Couce, Ridgwell, & Hendy, 2013), and concurrent phylogenetic analyses can elucidate if these habitat changes are phylogenetically constrained or not. Up to date, only one study has focused on how potential extinctions (based on IUCN criteria) will affect evolutionary diversity across the different reef ecoregions of the

world (Huang & Roy, 2015). However, whether the future shifts in corals' distribution are phylogenetically constrained or not, remains unexplored.

In this study, we used SDM techniques to predict the distributional shifts of 45 Atlantic scleractinian corals under a climate change scenario (A2 IPCC for the year 2100). We then explored whether these potential expansions, or contractions, are phylogenetically constrained. To reach this goal, we firstly assessed if distributional shifts (contractions/expansions) of 45 Atlantic reef-forming corals (scleractinian), and the main environmental variables driving their distributions, correlated with their phylogeny, i.e. whether expected contractions and expansions affected specific clades or not. Secondly, we estimated the potential richness and phylogenetic diversity loss and/or gain across the Atlantic, as well as the phylogenetic structure (clustered/overdispersed/random) of the communities and the taxonomic distinctiveness of the species, resulting from these distributional shifts.

Methods

Species records

A review of Atlantic scleractinian corals was carried out through internet databases and books. A search in the IUCN Red List was firstly filtered by the taxonomy (animal-cnidaria-anthozoa-scleractinia), and secondly by the location of the Atlantic FAO Marine Areas, including the northwest, southwest, western central and eastern central Atlantic. For these species, presence records were automatically downloaded using the R-Package "spocc" (Scott, Ram, Hart, & Chamberlain, 2017), an interface directly connected with occurrence data sources provided by the 'Global Biodiversity Information Facility' ('GBIF') and the 'Ocean Biogeographic Information System' ('OBIS'). Presence records were checked with the literature available on corals distribution (e.g. Veron et al. 2016). Additionally, presence records were revised and, if necessary, edited by removing duplicates, fossil records or erroneous data. Presence records separated by less than a pixel (0.25 decimal degrees) were also removed. Species with < 15 presence records were excluded. A final set of 45 species, covering 64% of Atlantic scleractinian corals, from which phylogenetic information was also available, was finally used (Fig. 1).

Environmental variables

Environmental data were downloaded, as raster layers, from the global marine data set 'Bio-Oracle' (Tyberghein et al., 2012), including minimal, maximal, mean and range values of sea surface temperature (Sst), Dissolved oxygen, pH, Salinity, Chlorophyll *a*, Diffuse attenuation (Da), phosphate, nitrate, and photosynthetically active radiation (Par) (Table S1). The distribution area, where corals presences were recorded, included all the American coasts and the Cape Verde Islands, restricted by a bathymetric mask of 100 m to include all records, whereas all the variables were rescaled to a resolution of 0.25º to match the biotic resolution. To avoid auto-correlated variables, a Spearman's correlation matrix was generated, and among the groups with $r_s > |0.80|$, the most important variables driving corals' biogeography were selected (Couce et al., 2012; J.A Kleypas et al., 1999). The predictors finally selected were: Damax, Parmax, pH, Phosphate, Salinity and Sstmean. Additionally, other exploratory analyses, as a cluster dendrogram based on a distance matrix, also discerned between the same 6 variables, with a threshold of 0.20 (inversely proportional to the Spearman's 0.80). Variance inflation factor (VIF) analyses, which measure the inflation of the unexplained variance as a consequence of correlation between variables (Belsley et al., 1980; Marx & Smith, 1990), showed values < 5.2, which are considered acceptable (Duque-Lazo, van Gils, Groen, & Navarro-Cerrillo, 2016). Therefore, the 6 variables were included as predictors in the SDMs.

SDMs

Forty-five SDMs, one for each coral species, were developed to project their 'current' and 'future' habitat suitability across the entire Atlantic. To generate the SDMs, the Maximum Entropy Modelling software (MaxEnt) was used. MaxEnt is a machine learning approach that correlates presence records with environmental gradients, by selecting the statistical model that maximizes the Entropy of the species probability distributions (Phillips et al., 2006). MaxEnt (Maximum Entropy) is the most widely used tool when absence data is not available. Response curves were fitted to be linear, quadratic and hinge. Extrapolations were allowed in the projections. The regularization and beta parameterization were explored choosing the default settings, since they represented the most reliable response curves to detect temperature thresholds after comparing a set of models. The final output of MaxEnt

was a raster map, projecting the habitat suitability for the entire Atlantic.

To evaluate the performances of the models, an internal data-splitting validation was applied, using 70% of the presence points for training and the rest (30%) for testing. The predicted area under the curve (AUC) was the performance estimator of the model. This measure is provided by the Receiver Operating Characteristic (ROC) curve from MaxEnt (DeLeo, J.M.; Campbell, 1990), which assess the sensitivity of the model as the fraction of presence records correctly classified as presences (true positives) against the fraction of absence areas incorrectly classified as presence (false positives) (Allouche, Tsoar, & Kadmon, 2006). AUC values > 0.85 indicate a good discrimination power (Phillips et al., 2006).

The habitat suitability of each species was determined under 'current' and 'future' conditions. The 'current' variables contained mean monthly values from years 2002 to 2009; the 'future' variables were extracted from the UKMO-HadCM3 model for the year 2100, which represents the A2 scenario conditions defined by the IPCC. The A2 is the most severe scenario among those provided by 'Bio-Oracle', with projected increases of temperature of 2.6 °C and CO_2 emissions >800 ppm until 2100 (Meehl et al., 2007). Only Sstmean and Salinity A2 2100 IPCC projections were available by 'Bio-Oracle'. Therefore, for the predictions, these future variables were included as inputs of the SDM along with the remaining 'current' variables (Damax, Parmax, pH, Phosphate); we assumed, therefore, that their current values will be maintained in the future. All projections were replicated 10 times and the final map was constructed by averaging all of them. Once the habitat suitability maps of all the species were generated, they were binarized into potential presence/absence areas accordingly to the maximum training sensitivity plus specificity logistic threshold (Cao et al., 2013; Liu, Berry, Dawson, & Pearson, 2005), assuming no dispersion limitations. Relative percentages of absence and presence areas respecting the total area of study were calculated. Then, areas of expansion/contraction for each species were calculated by extracting the values of the 'future' distribution relative to the 'current' maps.

Simulated potential 'current' and 'future' coral communities were then constructed with the two binarized maps of habitat suitability ('current' and 'future'). These maps were transformed into two

community matrices ('current' and 'future') with predicted species presence and absence for every pixel of their corresponding map. Species richness was calculated for each pixel of the 'current' and 'future' maps, and potential changes ('future' – 'current') were also calculated.

Phylogenetic analyses

A phylogenetic tree (in nexus format), including only the target species of our study, was obtained pruning the large coral molecular tree provided by Huang and Roy (2015), using the R-package 'ape' (Paradis & Schliep, 2018). Then, the evolutionary distinctiveness (ED) (Isaac, Turvey, Collen, Waterman, & Baillie, 2007), i.e. the originality or evolutionary isolation of each species in the pruned tree, was computed with the 'evol.distinct' function ('equal.splits' option) of the R-package 'Picante'(Kembel et al., 2010). The pruned tree was then transformed into a cophenetic matrix of phylogenetic distances, by computing pairwise distances between each pair of tips, using tree branch lengths through the R-package 'ape'. By means of non-parametric Spearman correlations, we tested for the significance of correlations between dissimilarities matrices of phylogenetic distances and expansion/contraction areas and the six main variables driving corals distribution, calculated by means of Euclidean distances. A total of 9,999 permutations were computed to test for the statistical significance of correlations (α=0.01). To support these analyses, we additionally constructed a phylogenetic tree in MEGA (Molecular Evolutionary Genetic Analysis version 7.0, Kumar et al. (2016), using GenBank sequences, and repeated the correlation analyses, obtaining the same results (not shown).

To understand potential changes in the evolutionary diversity of Atlantic coral communities under 'future' climatic projections, three phylogenetic metrics were computed. In particular, the Faith's Phylogenetic Diversity (PD), the Phylogenetic Species Variability (PSV) and the standardized PD (PD_{SES}) of the coral community from each pixel, under 'current' and 'future' conditions, were estimated. The Faith's PD accounts for the sum of all branch lengths connecting the species in a community (Faith, 1992); it was calculated with the 'pd.query' function of the R-package 'PhyloMeasures' (Tsirogiannis & Sandel, 2017). The PSV quantifies the degree of relatedness among species in the community (Helmus et al., 2007); values near 1 indicate that taxa are poorly related, while values approaching 0

reflect that taxa are closely related. PSV was calculated with the 'psv' function of the R-package 'picante'(Kembel et al., 2010). Resulting values of PD and PSV were then projected into geographic maps of 'current' and 'future' climatic conditions, and their differences mathematically computed. The PD_{SES} compares the observed PD to null communities generated by randomizations (Webb et al., 2008) to infer the phylogenetic community structure (clustered, overdispersed or random), in this case for each pixel of the map. Significant positive PD_{SES} values indicate phylogenetic overdispersion; significant negative values denote phylogenetic clustering (Kellar, Ahrendsen, Aust, Jones, & Pires, 2015); non-significant values otherwise indicate a random phylogenetic structure. The 'ses.pd' function of the R-package 'picante' was used to compute this measure. Standardized effect sizes estimate the divergence between the observed phylogenetic distances *versus* those of mean null communities, divided by the standard deviation of the phylogenetic distances in the null data; $PD_{SES} = \frac{[obs_{PD} - mean(null_{PD})]}{sd(null_{PD})}$ (Webb, Ackerly, McPeek, & Donoghue, 2002). The PD_{SES} and their associated observed z-score and p-values were calculated through 999 randomizations of the taxa labels across the tips of the phylogeny. Communities under phylogenetic clustering had p-values < 0.025; p-values > 0.975 indicated overdispersion; p-values between 0.025 and 0.975 denote communities are phylogenetically random.

Results

SDMs

The two main environmental variables driving the distribution of species, which most frequently appeared in the models according to the percent contribution and permutation importance, were 'Phosphate' and 'Sstmean' (Table S2). The lowest training AUC value from all the SDMs was 0.883 (Table S2), indicating a good performance for all modelled species. Thirty-one species, out of the 45, were predicted to expand their suitable habitat by the year 2100, under the A2 IPCC scenario (Fig. 1, Fig. S1). Eight species are predicted to expand their ranges in a percentage >10%. *Porites furcata* would potentially have the highest future range expansion (14%). The highest relative increment, with regard to current conditions, was predicted for *Mussismilia harttii*, i.e. from 2.8% ('current') to 11.5% ('future'). On the contrary, 14 species were predicted to

reduce their habitat by 2100; *Manicina areolata* exceeded a 10% contraction, and *Agaricia fragilis* had the highest relative reduction, from 9.2% ('current') to 1.3% ('future'). According to the predictions, species richness will decrease in some tropical regions; notably in the Caribbean Sea, some regions of Brazil, as well as in the coasts of the Gulf of Guinea in Africa. Conversely, some areas between the Caribbean Sea and Brazil, along with some regions at higher latitudes in America and Africa, will increase their richness.

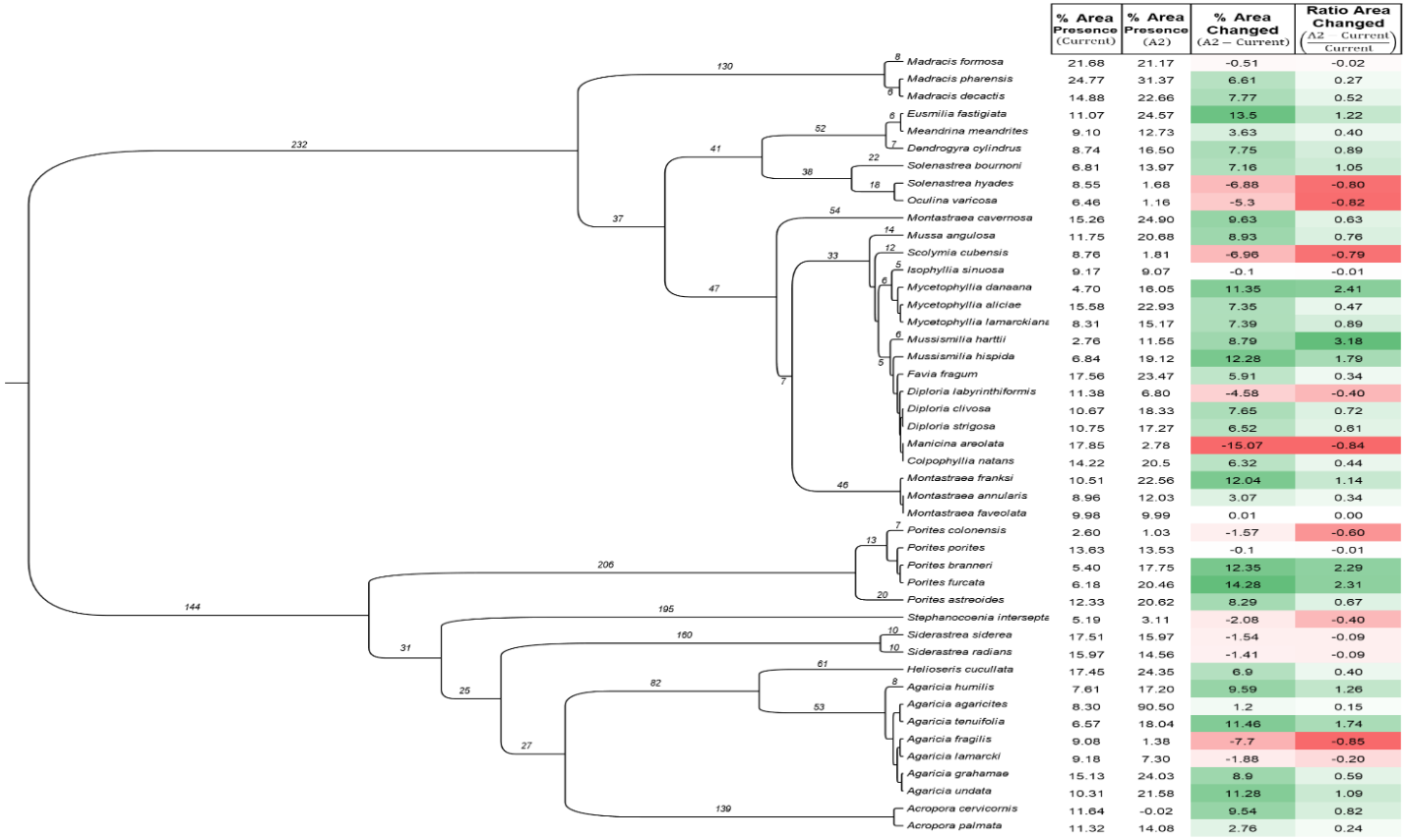

Fig 1. Phylogenetic tree of Atlantic corals. The numbers represent branch lengths (values < 5 were omitted). For each species, the percentage of area categorized as presence in the $Current$ and the $A2$ scenarios the percentage predicted by the SDMs ($\mathrm{A2} - \mathrm{Current}$) of contracted (negative values, reddish) or expanded (positive values, greenish) areas, is indicated. The ratio of this change is also included, e.g. if the value is +2, this means that the future suitable area will be double of the current area. If the value is -1, the habitat suitable for the species will disappear in the future. Negative values are represented in red, positive values in green, and no change (zero) in white.

Phylogenetic analyses

The Spearman correlation between dissimilarity matrices of phylogenetic distances and expansion/retraction areas of corals was non-significant (rho = -0.003, p-value > 0.2). As a result, predicted distributional shifts of corals are independent of their phylogenetic relationships. These shifts appeared randomly distributed across the phylogeny (Fig. 1); unrelated species exhibited similar habitat changes relative to closely related species. Similarly, variables driving the distribution of the species showed un-significant correlations with the dissimilarity matrix of phylogenetic distances (Table S3).

The change of PD from 'current' conditions to the year 2100 varied across the Atlantic (Fig. 2). Areas of increased PD coincided with areas where most species were projected to expand their ranges, e.g. most of the Gulf of Mexico, Florida (EEUU) and the North-western coast of Africa. Areas of decreased PD partially coincided with areas of decreased species richness (Caribbean, Brazil, Gulf of Guinea, Fig. 2), probably due to hot future temperatures (Fig. S2). A few exceptions included Nicaragua, The Bahamas and nearby islands, where the species richness increased, but the PD decreased. This was due to loss of few species with long internal branches (e.g. *Stephanocoenia intersepta*, a species with few close relatives, presenting the highest evolutionary distinctiveness, ED = 246.4, Table S4), and the gain of more species with short external branches (e.g. *Mycetophyllia aliciae*, ED < 5).

The PSV index majorly decreased in West Florida, the Gulf of Mexico, Cuba, Haiti, Honduras, Nicaragua, Panamá, half of north Colombia, the Guyanas and Surinam, eastern Brazil, most of the Macaronesian islands, Sierra Leona, Libera and Ghana. On the contrary, North and East Florida, Bahamas, the north of the Gulf of Mexico, North of Costa Rica, the other half of Colombia, Venezuela, the Lesser Antilles, some patches in Brazil, the western Canary Islands, Sahara, Guinea and the Gulf of Guinea increased their PSV. The rest of the areas maintained similar patterns of PSV under the A2 scenario relative to the current conditions.

Under 'current' conditions, only 0.25% of the pixels containing more than one coral species were phylogenetically clustered (PD_{SES} $p < 0.025$) (Fig. 3), while only one pixel (i.e. 0.03% of the pixels) was phylogenetically overdispersed (PD_{SES} $p > 0.975$). The rest of the pixels showed a

random phylogenetic structure (PD_{SES} $0.025 < p < 0.975$). The results for the A2 scenario showed a slightly higher percentage of phylogenetically clustered (0.65%) and overdispersed pixels (0.15%). However, this still represents a very small portion (Fig. 3), indicating that most of the communities have a random phylogenetic structure.

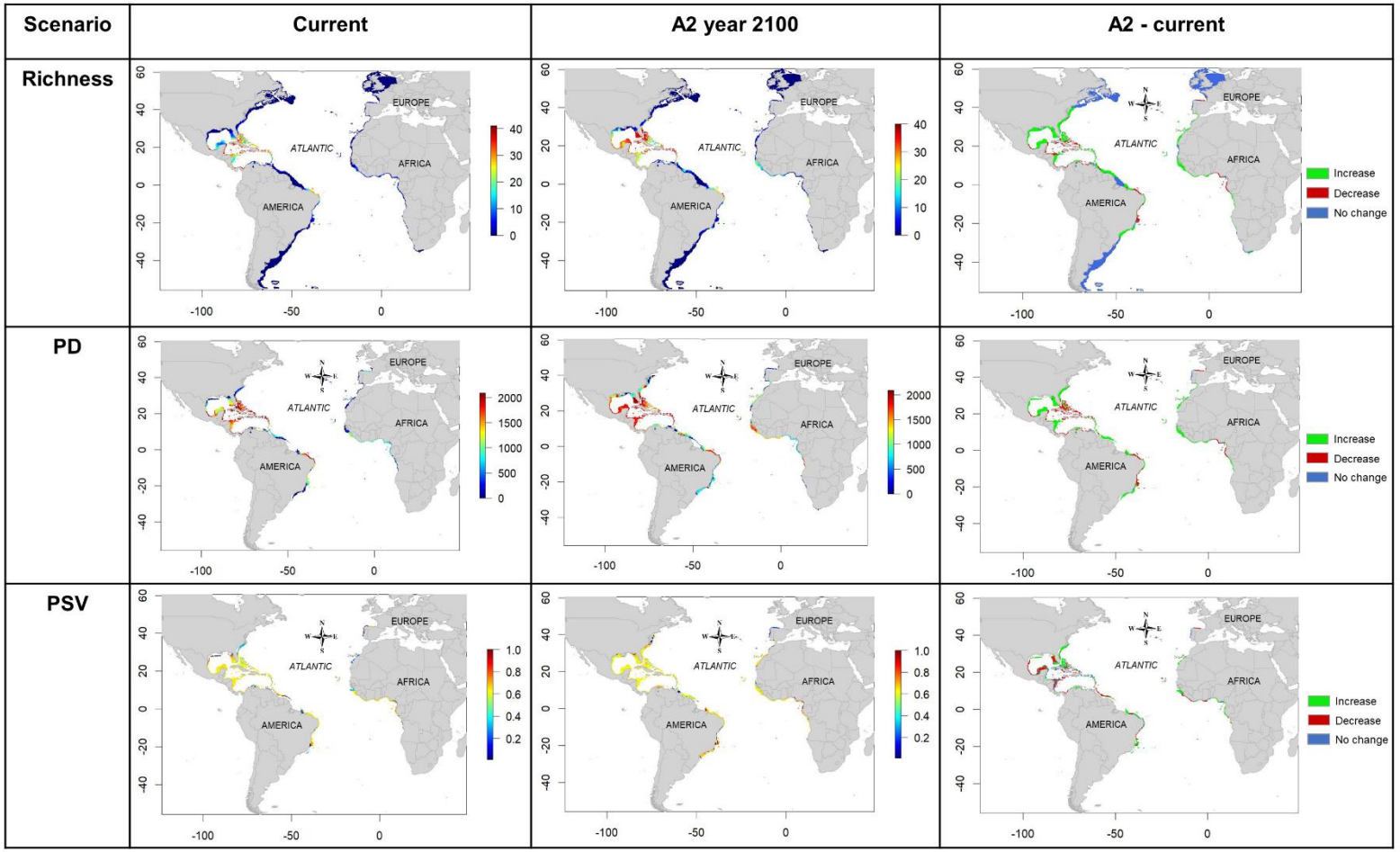

Fig. 2. Maps of evolutionary diversity of corals under 'current' (first column) and the A2 scenarios (second column). The third column shows changes from 'current' to 'future' conditions. Blue, green and red areas denote: no changes, increases and decreases, respectively, in the corresponding metric of diversity (species richness, PD and PSV).

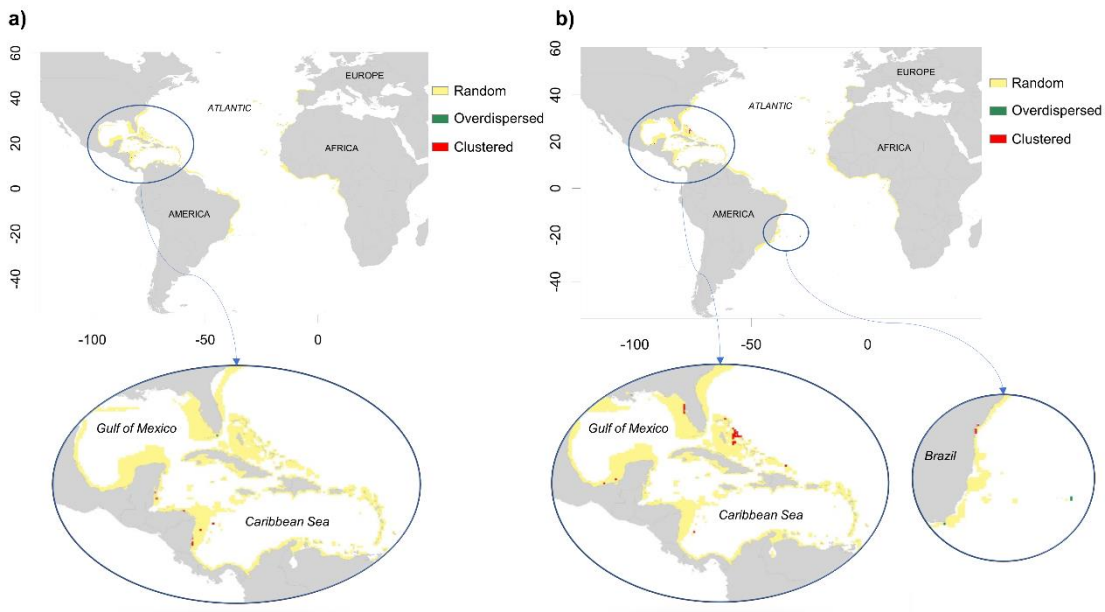

Fig. 3. Phylogenetic structure of coral communities under the (a) 'current' and (b) 'A2' scenarios. Areas considered as 'phylogenetically random' are in yellow, 'phylogenetically clustered' in red, and 'phylogenetically overdispersed' in green.

Discussion

Our results have shown that some Atlantic corals will decrease their suitable habitat by the year 2100, while others will expand their range. Despite the pattern of contractions differs among species, most species are projected to be contracted in tropical regions, coinciding with projected high temperatures in the future. Similarly, potential expansions are expected to be located at higher latitudes, where current temperatures are too cold for corals; due to global warming, however, temperatures will increase by the end of the century. These potential distributional shifts do not only affect the extinction risk of some species, but also change the species composition of certain marine communities. Changes in the species richness and phylogenetic diversity of corals across the Atlantic show how climate change can distinctly disturb their current diversity pattern, i.e. decreases in tropical areas and increases at high latitudes. These changes have important implications for the preservation of coral reefs, and the results presented here can help to set priority areas of conservation (Huang & Roy, 2015).

The two most important variables driving the distribution of Atlantic corals were 'Sstmean' and 'Phosphate'. These variables are directly connected with typical tropical conditions (J.A Kleypas et al., 1999), because low phosphate levels (~0.1) enhance corals' symbiosis, and low (~ <16 ºC) and high temperatures (~ >30 ºC) limit the photosynthesis of corals' symbiont (Coles & Jokiel, 1977; Glynn & D'Croz, 1990; Ove Hoegh-Guldberg, 1999; J.A Kleypas et al., 1999). However, beyond this general range of values, each species has slightly different preferences or tolerances, also depending on their location and their type of symbionts. Some species bleach at higher temperatures than others (Yee, Santavy, & Barron, 2008); e.g., branching corals are less resistant to bleaching than massive and encrusting corals (Loya et al., 2001). Since environmental tolerances vary across species, it is expected that phylogenetically related species would share similar environmental variation (Sunday et al., 2012). However, according to our results, there was not such phylogenetic connection. This c. Similarly, no correlation was found between projected distributional shifts of Atlantic corals and their phylogenetic relationships. Nearly all the communities across the Atlantic showed a random phylogenetic structure, as well as intermediate relatedness values (PSV). In summary, any potential retraction will not explicitly affect certain clades of coral species. In other words, the potential future loss of Atlantic corals will be randomly distributed across the phylogeny, alleviating an inordinate loss of evolutionary history (Heard & Mooers, 2000; Mace, Gittleman, & Purvis, 2003; Nee & May, 1997; Wilfried Thuiller et al., 2011).

The species whose habitats are going to decrease the most are: *Agaricia fragilis* and *Manicina areolata*. According to the IUCN, *Agaricia fragilis* has not enough information to be categorized under any conservation status (i.e. a data deficient species), while *Manicina areolata* is considered as 'least concern'. The evolutionary distinctiveness provided by our study sets *M. areolata* as the second species with the lowest score (ranking 44/45) and *A. fragilis* in the rank 32/45. This measure is often used to set conservation actions (Isaac et al., 2007; Redding & Mooers, 2006); species with high values are prioritized in terms of conservation (more distinct), whereas species with low values are left in the background. Additionally, both species are considered as 'weedy' (Darling et al.,

2012), which means they have high rates of growth and are prone to survive in non-favourable environments (Darling et al., 2012; Jackson & Hughes, 1985). In view of this, both species would not be considered as priority species for conservation. However, our results project a severe decline in their habitat; additionally, they have also experienced relevant decreases during the last decades. For example, *A. fragilis* decreased a 53% from 1975 to 1982 in Florida (Dustan & Halas, 1987). Rodríguez-Martínez et al. (2012) also reported a 9% decrease of *A. fragilis* colonies in the Mexican Caribbean reefs from 2006 to 2009. Other studies have informed about extensive bleaching impacts on both species; for example, in Bahamas, in 1998, 40% of the colonies of *M. areoalata* were affected by bleaching (Mcgrath & Smith, 2003). In Puerto Rico, *M. areolata* and *A. fragilis* suffered a severe bleaching event in 2005, which impacted the 100% of their colonies (Hernández-Delgado et al., 2006). These species might not be the most relevant from a distinctiveness perspective, but they are in decline, and, at least, they should be considered in future conservation decisions for the Atlantic. On the contrary, *Mussismilia harttii* and *Porites furcata* are two species, whose area of expansion will potentially increase by the 2100. These corals can be considered as 'winners' under future climatic scenarios, if their dispersion capacities allow them to reach new areas.

Interestingly, our study shows different patterns of diversity changes caused by climate change depending on the metrics. Remarkably, the areas with larger changes in coral richness do not exactly coincide with those of larger PD changes. Richness and PD maps show certain differences in Bahamas, South and East of Dominican Republic, Puerto Rico, and the northern Lesser Antilles, where richness increases, but PD decreases. Despite richness increases there, lost species have long internal branches, which caused a higher decrease of PD than the relatively small increase produced by the incorporation of new, but phylogenetically similar, species. For example, in the south of the Dominican Republic, species that are predicted to appear in the future scenario are species closely related to those that are predicted to persist under future conditions (Fig. S3). The appearance of *Montastraea annularis* slightly increases PD, because it is closely related to *Montastraea faveolata*, which is present under both scenarios. Something similar occurs with *Porites branneri*, relative to *Porites furcata*. Similarly, the disappearance of *Manicina areolata* is

practically imperceptible due to the persistence of a closely related species, *Colpophyllia natans*, both with very low evolutionary distinctiveness (ED). On the contrary, *Stephanocoenia intersepta*, present in the current scenario but absent under future predictions, lead to a relevant PD loss (Fig S3). This species belongs to an isolated and old clade with no closely related species, showing high ED (Table S4). The large ED of *S. intersepta* suggests its pre-eminent conservation worth, because this is a unique species, which has no other phylogenetically similar relative if becoming extinct (E. O. Wilson, 1992). Therefore, active conservation and restoration strategies, e.g. gene banks, artificial reefs via corals fragmentation, sexual assisted reproduction or transplantation (Young, Schopmeyer, & Lirman, 2012), will help to conserve this species and will avoid huge diversity losses in the future. On the other hand, the species shifts in this region produced an overall positive change in the PSV (Fig. 2), showing that the global relatedness of the species decreased with respect the current conditions. However, the future absolute values still represent no relevant relatedness among species.

Some areas show a decay in the projected PD, which is accompanied with a loss in PSV (e.g. Cuba, Jamaica, Haiti, Panama, and a small inner part of the Gulf of Mexico). In such areas, the removal of unique long branches is responsible for the main loss of PD; the elimination of short branches from one specific section of the phylogenetic tree causes a concurrent PSV decay (Huang & Roy, 2015). These zones tend to display high mean sea surface temperatures, where physiological thermal thresholds of some corals can be exceeded, e.g. *Millepora alcicornis* (Rodriguez, Garcia, Carreño, & Martínez, 2019); and future predictions of bleaching episodes are elevated (Donner, Skirving, Little, Oppenheimer, & Hoegh-Gulberg, 2005; Huang & Roy, 2015; van Hooidonk, Maynard, & Planes, 2013). Therefore, these geographical areas are of high vulnerability to climate change and thus of special interest for conservation.

Despite some relevant results obtained by this study, specially from a conservation perspective, some limitations need to be considered. Physiological thresholds in future conditions might be undetected by the MaxEnt response curves, so the use of Hybrid SMDs (see, Rodriguez et al., 2019) would be recommendable. The model is constructed only with presence data, and real absence data would improve confidence. This is particularly pertinent in

areas where sampling effort is low, e.g. on the coasts of Africa. This is of special interest when generating the matrices of species composition for the diversity analyses, because the threshold chosen for making binary predictions can produce an overprediction in species richness (Benito, Cayuela, & Albuquerque, 2013; Dubuis et al., 2011; Schmitt, Pouteau, Justeau, de Boissieu, & Birnbaum, 2017). SDM maps are based on habitat suitability indices, which do not assure that a species is currently present in an area, because of biotic factors, e.g. dispersal capacity, or competence with other species. This is the case of northern Spain, which is projected as a suitable area for the presence of some corals, although this region is currently habited by macroalgae, one of the main corals' competitors. Nonetheless, the cover of frondose, erect, macroalgae in northern Spain is currently (and projected to be) in decline due to warming temperatures (Duarte et al., 2013; Franco et al., 2017; Martinez et al., 2015; B. Martínez et al., 2012), so this opens an opportunity for tropical corals to compete if they reach these latitudes within the next decades, via ocean currents or anthropic routes of dispersion. In this sense, the tropical hydrocoral *Millepora alcicornis* arrived to the Canary Islands in the last decade (Clemente et al., 2010), which according to some predictions could also expand its range to higher latitudes (Rodriguez et al., 2019). Hence, we must be aware that the use of SDMs have some limitations, but these tools are still useful when no field samplings are available and future projections are needed, generating relevant information at broad scales.

In summary, the richness and the phylogenetic diversity of Atlantic corals from certain areas will be more compromised than others by the effects of climate change. Some Atlantic areas could lose a considerable amount of PD, particularly in the Caribbean, the central coast of Brazil and the Gulf of Guinea. However, other areas, mostly at higher latitudes and the western African coasts, could increase such PD. The areas in decline can be considered as priority areas for conservation, which are usually affected by bleaching events, e.g. central Caribbean (Eakin et al., 2010; A. Winter, Appeldoorn, Bruckner, Williams Jr., & Goenaga, 1998). Despite certain regions may lose many species (richness decrease), if the total length of the phylogenetic branches lost is small, the negative effect can be offset by the inclusion of new species with longer branch lengths. Notably, some species, as *Stephanocoenia*

intersepta, when disappear from an area, contribute more to a quantitative decrease of PD because they belong to isolated old clades (high ED), than relatively young and redundant species. Conservation of such critical species can help to preserve the diversity of certain communities, if remaining species do not suffer a massive decline. Conservation efforts can also be focused on species with low ED (e.g. *Colpophyllia natans* or *Manicina areolata*), because they are able to regenerate novel diversity rapidly (Crozier, 1997; Erwin, 1991; Isaac et al., 2007). Detection of potential areas of significant loss of phylogenetic diversity, under climate change scenarios, is crucial to evaluate and protect the future of coral reefs.

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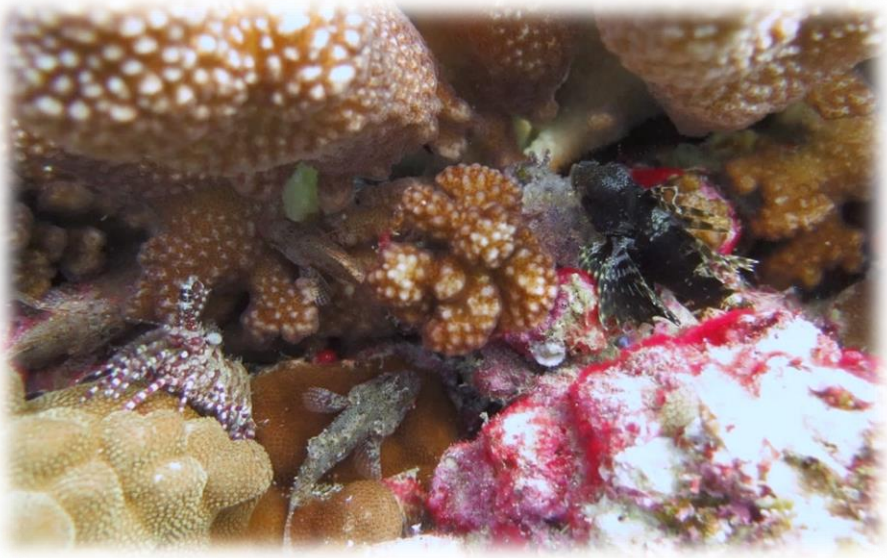
CHAPTER 4

Integration of physiological knowledge into Hybrid Species Distribution Modelling to improve forecast of distributional shifts of tropical corals



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Integration of physiological knowledge into hybrid species distribution modelling to improve forecast of distributional shifts of tropical corals

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Abstract

Aim: Predicting species distributional shifts in future climate scenarios representing conditions that do not exist in the current world is a challenge. Species distribution models may result in misrepresented projections for species living in extreme conditions if based on truncated response functions. Model extrapolation may not detect declines that could occur if future environment conditions exceeded the physiological tolerance of the species. We developed a novel method aimed to overcome this constrain by incorporating the physiological response function of a tropical hydrocoral to temperature as a predictor variable in a Hybrid SDM. **Location**: Atlantic Ocean.

Methods: We conducted ecophysiological experiments simulating heat and cold stress to determine the maximum photochemical efficiency of the hydrocoral's symbiont along a thermal gradient to identify sublethal and lethal conditions. The response curve obtained was then applied to a temperature raster to create a new physio-climatic variable, which was integrated into the Hybrid SDM as a predictor. Simple Physiological and Correlative SDMs were compared with the Hybrid model.

Results: The Hybrid SDM outperformed the Correlative SDM allowing predictions without extrapolations in the physio-climatic predictor. It suggested habitat contractions in tropical regions with forecasted temperatures above the coral's physiological tolerance, which were underrepresented by the Correlative SDM. It also incorpo-rated habitat suitability restrictions by other predictors of unknown physiological response by incorporating correlative information (as limitations in river mouths by low salinity). In this way, by integrating mechanistic and correlative knowledge, the Hybrid SDM also predicted a potential expansion to higher latitudes, which agreed with the recent evidence of its expansion into the subtropical Canary Islands.

Main conclusion: Integrating physiological knowledge into Hybrid SDMs by adding a physio-climatic predictor improves model transferability resulting in predictions of decline in future climates, which may be misrepresented by SDMs trained at present-day conditions, and therefore are advisable for early warning in conservation management.

KEYWORDS
climate change, conservation, ecophysiology, hybrid species distribution models, marine biodiversity, *Millepora alcicornis*

1 | INTRODUCTION

Global warming is driving rapid shifts in the distribution of species worldwide (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). Our ability to accurately predict these changes allows a realistic forecast of potential retractions and expansions in the distributional ranges of species. Species distribution models (SDMs) are powerful predictive tools that consider the correlations between the actual distributional records of organisms and the environmental variables that control their distribution, estimating the habitat suitability for a species along existing environmental gradients (Guisan et al., 2013; Pearson & Dawson, 2003). SDMs can generate projections at different spa-tial and temporal scales by extrapolating species responses into future or past climatic scenarios (Franklin & Miller, 2010). Hence, these tools have been employed for predicting the probability of ex-tinction of various taxa in several regions of the world, for example, plants, birds and frogs (e.g., Thomas et al., 2004), the spread of inva-sive species (e.g., Václavík & Meentemeyer, 2012), and for identify-ing potential climatic refugia under adverse scenarios (e.g., Martínez, Viejo, Carreño, & Aranda, 2012). SDMs have also been used to sup-port conservation planning decisions (e.g., Guisan et al., 2013), such as the creation of new protected areas (e.g., Leathwick et al., 2008).

SDMs have many applications but they also have important limitations, especially when making projections for new regions or fu-ture climates (Elith & Leathwick, 2009; Thuiller, Brotons, Araújo, & Lavorel, 2004). Uncertainty increases when the species' responses to the climatic predictors need to be extrapolated to higher or lower values than the environmental gradient where the model was trained, in some cases because future conditions are uncommon or do not currently exist. In these projections, some statistical methods keep as a constant the last suitability value obtained from model predic-tors, for example, clamping in maximum entropy modelling (MaxEnt; Phillips, Anderson, & Schapire, 2006), whereas others extrapolate suitability as the last trend of the predictor response curve. When last suitability value is relatively high or trend is increasing, projec-tions may fail by classifying as suitable regions where the projected environmental conditions will exceed the physiological tolerance for species survival (Anderson, 2013). Approximately 15 different cor-relative techniques are used in SDMs, such as random forests (RF), MaxEnt or generalized linear models (GLMs), but none of them can deal with this problem because they do not include specific terms incorporating the biological mechanisms driving the distributional limits of species (Buckley, Waaser, MacLean, & Fox, 2011; Martínez, Arenas, Trilla, Viejo, & Carreño, 2015).

Characterizing the physiological responses of species to climate and physical stress is the mechanistic basis for modelling their geographic distribution, including SDMs (Bozinovic, Calosi, & Spicer, 2011; Kearney & Porter, 2009). To investigate the mechanisms that explain tolerance limits, experiments that simulate stress conditions have been used routinely to obtain species response functions. These functions represent the physiological state of an organism along an environmental gradient including future conditions that do not currently exist. After obtaining the response curve, the spe-cies' threshold for survival can be determined and applied to the map of the physical variable, thereby predicting whether a species may become extinct under different climatic scenarios if the toler-ance threshold is exceeded (Deutsch et al., 2008), but this model-ling approach standing alone seems uncertain (e.g., Martínez et al., 2015). Only few studies have attempted to compare correlative SDMs projections with either those that apply thermal thresholds (Diamons et al., 2012; Gerick, Munshaw, Palen, Combes, & O'Regan, 2014; Martínez et al., 2015), biophysical models (Kearney & Porter, 2004; Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009), process-based models (Morin & Thuiller, 2009) or physiologically mod-els of extinction (Ceia-Hasse, Sinervo, Vicente, & Pereira, 2014). For example, Hijmans and Graham (2006) compared the predictions obtained by a mechanistic model after translating physiological in-formation for 100 plant species into suitability indices, with those from SDMs. This and similar studies of trees by Austin, Smith, Van Niel, and Wellington (2009), beetles by Sánchez-Fernández, Aragón, Bilton, and Lobo (2012), and seaweeds by Martínez et al. (2015) found significant correlations between upper and lower thermal tolerance limits observed in experiments and response curves built from SDMs. Therefore, it seems reasonable to support the math-ematical integration of both approaches (mechanistic and correlative) in the so-called Hybrid SDMs that has emerged just recently (see Dormann et al., 2012, and references therein). Albeit possible, Hybrid Modelling is uncommon and complex (see Talluto et al., 2016). One potential method outlined and developed by Elith, Kearney, and Phillips (2010) for toads, and similarly applied by Buckley et al. (2011) and Mathewson et al.. (2016) for butterflies and the American pika, respectively, proposes using the output of a mechanistic model as the input layer into a correlative SDM. In line with this research, we develop one of the few examples of a physiologically based Hybrid Distribution Model, specifically incorporating a new physio-climatic predictor into the model of a marine tropical hydrocoral. This ap-proach allows realistic predictions in future climate scenarios non- analogous to present-day conditions.

Tropical coral reefs are among the most diverse marine ecosystems throughout the world but also one of the most vulner-able to climate change (Hoegh-Guldberg, 1999). One-third of reef-building corals are considered to be at risk of extinction (Carpenter et al., 2008). Impacts on the foundational species that define the community structure (corals and hydrocorals) can lead

to large-scale losses of global biodiversity (Carpenter et al., 2008). Seawater temperature seems to be the main driver of coral biogeography, controlling many physiological processes that affect the normal functioning of corals such as respiration and calcification. Low temperatures, below ~16°C, cause internal damage to the photosynthetic apparatus of the symbiont inducing the mortality of the coral (Saxby, Dennison, & Hoegh-guldberg, 2003). These temperatures are usually associated with high latitudes restrict-ing the distribution of tropical corals to those limits. On the other hand, at the central areas of their distribution, corals live close to their upper thermal limit, thus high water temperatures may drive bleaching events involving the loss of symbiotic algae, which may ultimately cause their death (Douglas, 2003). Global warming has caused unusual and accelerated modifications of the geographic distributions of tropical corals, by leaving vacated regions with extremely hot temperatures, as in some parts of the Australian Great Barrier Reef, where some degree of bleaching affected 93% of corals (Hughes, Steffen, & Rice, 2016). On the other hand, pole-ward shifts of tropical currents that transfer warm conditions to subtropical and temperate latitudes are allowing corals to expand their ranges (Yamano, Sugihara, & Nomura, 2011). In particular, the hydrocoral *Millepora alcicornis* (Linneaus, 1758) has recently estab-lished in the Canary Islands (Macaronesia), far north of its tropical distribution (Clemente et al., 2010), possibly by means of drifting material from the Caribbean Sea (Jokiel, 1989; López, Clemente, Almeida, Brito, & Hernández, 2015). Due to its stony skeleton and fast growth, this structural species (Huston & Huston, 1994) con-structs a framework that serves as habitat for hundreds of tropical marine organisms in its native range (Lewis, 2006).

The aim of this study was to obtain a realistic prediction of the future habitat suitability of *M. alcicornis* under climate change scenarios representing conditions that do not currently exist. We developed a Hybrid SDM by integrating physiological information into a Correlative SDM and compared its results with those obtained using only a Correlative model on the one hand, and a Physiological model on the other. We hypothesize that the potential area inhabited by *M. alcicornis* will increase to occupy higher latitudes due to global ocean warming. Besides, a range retraction is also expected in tropi-cal areas where future temperatures will feasibly exceed the thermal tolerance of this hydrocoral. We anticipate that only models fed with physiological information will be able to predict such retractions in distributional ranges, representing early warning tools for conservation management. First, we conducted physiological experiments by simulating heat and cold stress to obtain a thermal response curve for *M. alcicornis*. The bell-shaped response curve obtained was then applied to a temperature raster to create a new physio-climatic predictor, which was integrated into the Hybrid SDM. Finally, we projected the Hybrid SDM using the conditions of IPCC scenarios (year 2100) and compared the results with the current model to detect changes in habitat suitability. Our study demonstrates that projections obtained by correlative SDMs can be improved when physiological information about species is integrated by adding a physio-climatic variable to the list of predictors.

2 | METHODS

2.1 | Distributional records

Presence records for *M. alcicornis* were downloaded from the Global Biodiversity Information Facility (GBIF) and the Ocean Biogeographic Information System (OBIS) web portals. Additional presences were obtained from the scientific literature and from underwater videos kindly provided by the non-profit organization OCEANA. A total of 1,201 records were compiled, most (>90%) corresponding to obser-vations taken from 1990 to 2011. Duplicate records and points less than 0.25° apart were removed using ArcGIS, to a final number of 159 reliable presences, that extended from Bermuda to the Brazilian coast of Rio de Janeiro in the western Atlantic Ocean, with maxi-mal prevalence in the Caribbean islands, Ascension Island, and the coasts of Central America and Florida. Several presence records in the eastern Atlantic Ocean included the Cape Verde Islands, but no records were found on the African Coast (Figure 1a).

2.2 | Environmental predictors

To characterize the main environmental gradients in the ocean, we initially compiled 23 variables from Bio-ORACLE at 0.25° resolution (Tyberghein et al., 2012) (Supporting Information Table S1). All variables were restricted to a depth of 100 m to exclude ocean areas far outside the potential seabed habitat for the coral. To avoid excessive autocorrelation among the predictors, we se-lected for modelling a short list of variables with Spearman pair-wise correlation coefficients <0.7. We selected a set of six final predictors: Sstmean that controls most physiological processes, particularly bleaching (Coles & Jokiel, 1977; Douglas, 2003); Salinity, because corals have osmoregulatory limits (Berkelmans, Jones, & Schaffelke, 2012; Ferrier-Pagès, Gattuso, & Jaubert, 1999); Maximum photosynthetic active radiation (Parmax), which drives the photosynthetic response of the symbiont (Halldal, 1968); Maximum diffuse attenuation (Damax), as an estimator of the turbidity of the water column that decreases irradiance (Kirk, 2010) which impacts coral's health (Fabricius, 2005); Nitrate, as eutrophic waters increase bleaching effects (Koop et al., 2001); and pH, because decreases may cause the decalcification of reef- building corals (Anthony, Kline, & Dove, 2008).

2.3 | Correlative SDM

Presence records were linked to the final list of uncorrelated environmental variables using MaxEnt 3.3.3k. Background locations were randomly distributed using the *add samples to the background* setting of MaxEnt within the same extent of the environmental layers. Features were set to allow linear and quadratic responses, and the importance of each variable measured by the percentage contribution index (Phillips et al., 2006). As the choice of statistical modelling method may affect the selection of the significant pre-dictors, we

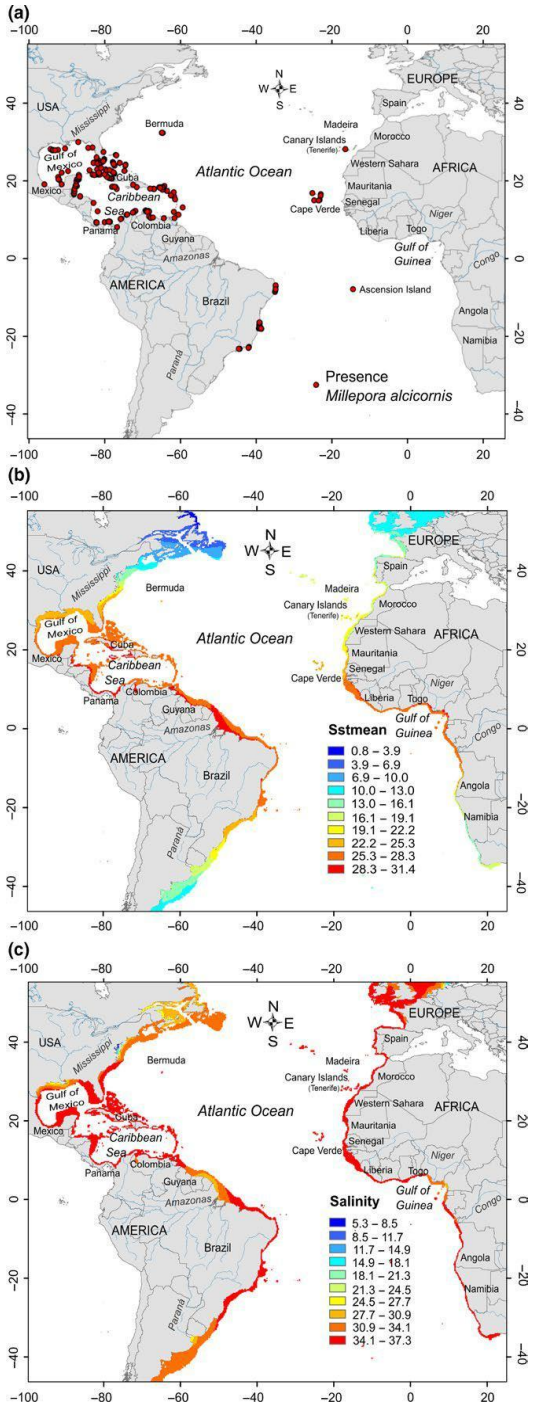

FIGURE 1 (a) *Millepora alcicornis* presence records in the Atlantic Ocean. (b) Mean sea surface temperature (Sstmean), and (c) Salinity maps downloaded from Bio-ORACLE (Tyberghein et al., 2012), restricted to a bathymetry of 100 m, and rescaled to 0.25° resolution

on pseudoabsences and quadratic terms, and then estimating the importance of each variable with the function *get_variables_importance* (Thuiller, Georges, & Engler, 2013); and using random forest (Kuhn, 2015), and the *importance* function (Liaw & Wiener, 2002). To create a consensus and parsimonious final model, we excluded the variables whose importance indices were below 20% in any of the three aforementioned approaches (Supporting Information Table S2). The final model including only two significant variables (see Section 3) was run in MaxEnt to project the habitat suitability in current and future scenarios, as this method has robust support for presence-only data (Elith et al., 2006).

2.4 | Functional response curve to temperature

Two experimental trails lasting 2 months each were done to determine the tolerance of *M. alcicornis* to cold and warm temperatures, respectively. The coral fragments (3–10 cm in height) provided by the Madrid Zoo Aquarium were pre-incubated indoors in a nurs-ery tank for 1 month at 26°C by means of an automatic tempera-ture control system (instrumental standard error of ±0.5°C) and at 12:12 hr photoperiod. Water condition was maintained optimal throughout the pre-incubation and subsequent experimental trails: salinity = 34.4 ppt, pH = 8.0–8.6, alkalinity KH = 1.7–4.5, Calcium Ca^{2+} = 350–450 ppm, Magnesium Mg^{2+} = 1,200–1,400 ppm, and low concentrations of inorganic Nitrogen and Phosphorous (NO^{3-} < 0.25 ppm, NO^{2-} < 0.3 ppm, NH^{4+} < 0.1, PO_4^{3-} < 0.5 ppm).

Starting in March 2015, we tested the response to cold temperatures by placing 30 fragments in three independent 25-L tanks (10 per tank) and lowering the temperature by 2°C each week until reach lethal conditions. On May 2015, exactly the same experimental design was used in a second trial using 30 new fragments, but in this case, the temperature was increased in 2°C steps until death.

The maximal quantum yield of photosynthesis (*Fv*/*Fm*) using a pulse amplitude modulated (PAM) fluorimeter, after dark ad-aptation for 20 min., was measured in two replicate readings as a proxy of the maximum photochemical efficiency of photosystem II. Decreases in *Fv*/*Fm* are representative of physiological stress in endosymbiont algae (Maxwell & Johnson, 2000; Roth, 2014). Small background signals indicate the absence of coral symbionts but the presence of endolithic algae on the dead skeletons. The photosynthetic response to temperature was fitted using two logistic curves, corresponding to ascending and declining temperatures, linked by a stable plateau representing optimum levels (modified from Thornton & Lessem, 1978), with MATLAB software using the equation:

$$Fv/Fm(T) = \frac{a}{(1+\exp(-b*(T-c)))*(1+\exp(d*(T-e)))}$$

, where T is the temperature, a is the curve's maximum value, b is the slope of the ascending curve, c is the temperature value for the ascending sigmoid's mid-point, d is the slope of the descending curve, and e is the temperature value for the descending sigmoid's mid-point. Any potential tank effect was discarded by comparing the Akaike information criterion (AIC) for the

2.5 | Hybrid SDM

The bell-shaped curve relating *Fv*/*Fm* to temperature was applied to every pixel of the mean Sea Surface Temperature (Sstmean) raster to produce a new layer called "Yieldsstmean." Thus, we obtained a map reflecting potential *Fv*/*Fm* for every pixel. For example, a pixel of the raster Sstmean with a temperature value of 25°C was transformed into a potential *Fv*/*Fm* value of 0.588 in the new Yieldsstmean raster, suggesting optimal conditions, whereas too cold or warm conditions for coral survival both resulted in low values. This new physio-climatic variable was included as one predictor in the MaxEnt Hybrid SDM, as well as the Salinity layer, while other variables were found irrelevant (see Section 3). We then compared the: (a) the MaxEnt map modelled with the mentioned combination of the physio-cli-matic variable "Yieldsstmean" and Salinity as predictors (*Hybrid SDM*); (b) the MaxEnt map modelled with the environmental vari-ables Sstmean and Salinity as predictors (*Correlative SDM*); and (c) the map generated by applying the physiological curve (*Fv*/*Fm*) to the variable Sstmean, that is, the map of "Yieldsstmean" (*Physiological model*).

We then binarized all the maps by dichotomizing the habitat suitability indexes using specific threshold values to represent poten-tial presence/absence areas. The correlative and hybrid maps were binarized using the average of the "maximum test sensitivity plus specificity logistic threshold" obtained with MaxEnt from 10 model replicates. To binarize the Physiological model, an Fv/Fm threshold of 0.3 associated with the values for the descending and ascending sigmoid's mid-points (corresponding to 15.7 and 31.7°C, see Section 3) was applied to Yieldsstmean.

2.6 | Projections

We used the Correlative (Salinity and SSTmean) and Hybrid (Salinity and Yieldsstmean) SDMs trained with MaxEnt in the native area (American coast and Cape Verde Islands) to project the potential presence areas on the coasts of Western Africa (no available records), the Canary Islands (recent introduction) and Western Europe (absent). We applied the current conditions and three forecasted IPCC SRES scenarios based on the Coupled Model Intercomparison Project (CMIP3, Meehl et al., 2007): the B1 (stabilization of atmospheric CO_2 concentrations at 550 ppm), A1B (720 ppm stabilization) and A2 (most severe: 800 ppm) for 2100 as downloaded from Bio-ORACLE (Tyberghein et al., 2012). When predicting with the Hybrid model, we also applied the trans-formation using the physiological response curve to the SSTmean projected layers, obtaining three projected Yieldsstmean rasters (for B1, A1B and A2). Extrapolations were enabled with MaxEnt to allow projections in areas with environmental values outside the limits of the training data. The clamping function was also ap-plied where extrapolated values were treated as if they were at the limit of the training range. Then, the areas where the projec-tions fell outside the range of the training data were inspected using the most dissimilar variable (MoD) map provided by MaxEnt, thereby indicating the variable furthest outside its training range (Elith et al., 2010). Regarding projections under the Physiological model, the physiological response curve (*Fv*/*Fm*) was applied to the Sstmean layers forecasted for the three IPCC scenarios, and then the maps binarized applying the *Fv*/*Fm* threshold of 0.3.

Four habitat categories arise by comparing current versus forecasted maps of habitat suitability: (a) presence: area categorized as presence in current and future scenarios; (b) absence: area categorized as absence in both scenarios; (c) new presence: area categorized as absence in the current scenario that changed to presence in the future scenario; and (d) new absence: area categorized as presence in the current scenario that changed to absence in the future scenario, representing a loss of suitable area. The areas corresponding to each category were transformed into percentages of the total studied area for the Hybrid, Correlative and Physiological models within the three scenarios of the IPCC (B1, A1B, A2) to allow comparisons (Supporting Information Table S3).

2.7 | Model evaluation

Models were assessed based on the current climatic scenario by calculating the Sensitivity (ratio of grid cells containing presence points correctly classified in presence areas), Specificity (ratio of pseudo-absences correctly classified in absence areas), Omission error (ratio of presence records wrongly classified) and Commission error (ratio of pseudoabsences wrongly classified) (Fielding & Bell, 1997). The "Correlative" and "Hybrid" models, both fitted by MaxEnt, were also tested using the regularized training gain (gain) and the area under the curve (AUC) of the receiver operating characteristic (ROC) plot as calculated by the MaxEnt software. The gain of the Physiological model was calculated using the function "*gains*" of the R pack-age "gains," and the AUC using the function "*auc*" of the package "pROC"(Robin et al., 2011). Ten replicates of an internal data par-titioning procedure (Fielding & Bell, 1997) were computed for the Correlative and Hybrid models by bootstrapping, where 70% of the points were randomly selected for training and 30% for validating. The geographic transferability performance was also assessed by partitioning the data using a geographic criterion, that is, data at the Northern Hemisphere (90% of presences) were used for training the model and those at the Southern Hemisphere (10%) for validating.

3 | RESULTS

3.1 | Correlative SDM

Among these six environmental predictors, only Sstmean and Salinity contributed more than 20% to the MaxEnt, GLM and random for-est models and thus were the only used in projections (Supporting Information Table S2). The SDM response curves for these variables showed that Sstmean >30°C and Salinity >36 PSS produced high habitat suitability values (~0.7), whereas temperature <20°C and Salinity <33 PSS reduced the habitat suitability to a low level (~0.2) (Supporting Information Figure S1a).

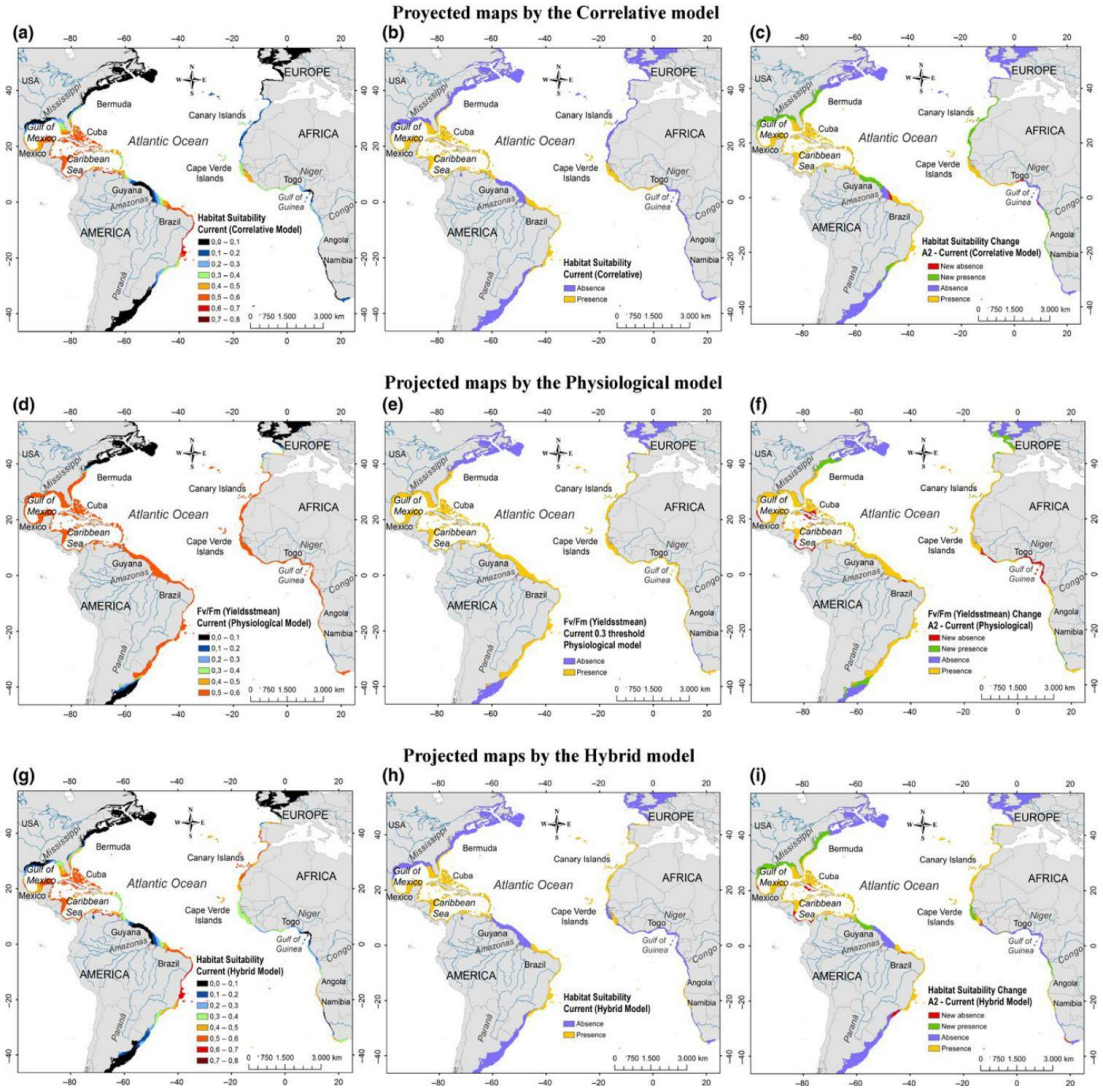

FIGURE 2 Projected maps of the habitat suitability of *Millepora alcicornis* in the Atlantic Ocean by applying the Correlative (a–c), Physiological (d–f) and Hybrid models (g–i), using 10 replicates in MaxEnt to obtain mean values for the Correlative and Hybrid models, and the physiological response curve in the Physiological model. The maps shown in the left column represent the habitat suitability projections (a and g) and the *Fv*/*Fm* (Yieldsstmean) (d) using the scenario of current climatic conditions. The maps in the central column were obtained binarizing those in the left column by applying the logistic threshold of Maximum Test Sensitivity Plus Specificity for habitat suitability (0.27 in b, and 0.29 in h); and the threshold *Fv*/*Fm* value of 0.3 in e; the blue colour indicates areas of potential presence and the black represents areas of potential absence. The maps in the right column show the potential changes in habitat suitability in the future climatic scenario of IPCC A2 compared to the binarized current scenario (central column), new areas of potential presence are in green and new areas of potential absence in red

After running MaxEnt with present-day layers of Sstmean and Salinity and binarizing the maps, that is, the Correlative SDM, the areas categorized as presence corresponded to the Gulf of Mexico, all the Caribbean Sea, the middle coast of Brazil and Cape Verde, which matched with the actual distribution of the species, but also the coasts of Guinea, Sierra Leone and Liberia with no presence records (Figure 2a,b). In addition, the model classified as potential presence areas the westernmost islands of the Canary Islands, including Tenerife, were *M. alcicornis* was found recently (Clemente et al., 2010). The model correctly explained the current distribution of the species, and thus, Sensitivity was high (0.93, Table 1), as well as identified unexplored and potentially new presence areas on the

TA B LE 1 Contingency validation table

	Correlative model		Physiological model	Hybrid model	
	Internal validation	Geographic transferability	Validation[a]	Internal validation	Geographic transferability
Sensitivity	0.93	0.90	1.00	0.88	0.92
Specificity	0.56	0.58	0.37	0.59	0.56
Omission error	0.07	0.10	0.00	0.12	0.08
Commission error	0.44	0.42	0.70	0.41	0.44
AUC-ROC[b]	0.83	0.85	0.59	0.81	0.95
Gain[c]	0.82	0.37	0.33	0.75	0.63

Note. Sensitivity and Specificity, calculated as the ratio of presence records and pseudoabsences correctly projected, respectively. Omission and Commission errors, as presences and absences wrongly predicted, respectively. Results obtained by the three different models (Correlative, Physiological and Hybrid) are shown.

[a]The Physiological model had neither internal validation nor geographic transferability as not fitted using MaxEnt. [b]The AUC-ROC of the Physiological model was developed using all the presences and the double of pseudoabsences. [c]The gain for the Physiological model was obtained by the package "gains," whereas for the Correlative and Hybrid models the regularized training gains were obtained by MaxEnt.

African coasts. Most absence areas were also correctly classified comprising the northern coasts of the Gulf of Mexico, the coasts of Guyana, Surinam, French Guiana, north–south Brazil, and most African and European coasts (Figure 2b), due to the low salinity values in river mouths and the low temperatures at high latitudes (Figure 1b,c), resulting in fair Specificity (0.56, Table 1). These results were further supported by the geographic transferability validation obtaining similar Sensitivity and Specificity values (0.90 and 0.58, respectively, see "Correlative model" in Table 1).

Projected distributional patterns were similar among the three future scenarios (B1, A1B and A2) (compare Figure 2c and Supporting Information Figure S2a,b; and values in Table S3), and thus, the most severe future scenario (A2) is used to explain the results. The Correlative SDM, using the A2 scenario, predicted that 38.7% of the territory studied by the year 2100 will be repre-sented by presence areas, of which 14.8% will become new pres-ence areas relative to the current projection. This increase in the potential area of occupancy will be partially located on the coasts of USA, in the north of the Gulf of Mexico, on the coasts of Guyana and Surinam, on the coast of Angola and north of Namibia, from the coasts of Morocco to Senegal, and the eastern islands of the Canary Islands, Madeira and south of Spain. On the other side, new contractions comprising small new absence areas were evident in the north of Brazil, as well as in Togo and Benin representing 0.9% of the territory (Figure 2c, Supporting Information Table S3).

3.2 | Physiological model

The estimates of the coefficients *c* and *e* in the bell-shaped response curve, that is, the temperature values for the mid-points of the as-cending and descending sigmoid, were 15.7 and 31.7°C, respectively, suggesting rapid decreases in *Fv*/*Fm* below 0.3 at these two tem-peratures (Figure 3). Therefore, this threshold value was considered a good proxy of lethal conditions and, as mentioned, was applied to the map of the physio-climatic predictor Yieldsstmean (Figure 2d) to estimate the potential areas of presence–absence (Figure 2e). When comparing this map with that from the Correlative SDM, high habitat suitability was suggested at latitudes between 40°N and 40°S over-estimating the actual extent of the species, and thus, Sensitivity was 1, but Specificity the lowest among models (0.37, Table 1). Absence areas by low salinity conditions detected by the Correlative SDM were misclassified as this physiological response was not investi-gated experimentally (in this study or previously) and thus could not be considered.

The overestimation of presence areas by this model was also ev-ident in the forecasted map for the IPCC scenario A2, where pres-ence areas represented the 48.9% of the total territory (Supporting Information Table S3), including new presence areas to higher lat-itudes than those suggested by the Correlative SDM (compare Figure 2c,f), that would fell within the physiological thermal toler-ance of the species when other limiting factors are not accounted for. On the other hand, the Physiological model predicted significant absence areas including much of the Gulf of Mexico, the Caribbean Sea and the Gulf of Guinea, suggesting forecasted situations of high lethal temperature conditions not detected by the Correlative SDM along the centre of distribution of *M. alcicornis*.

3.3 | Hybrid SDM

Yieldsstmean and Salinity were used in the Hybrid models because they contributed more than 20% to the MaxEnt algorithms (58.5% and 33.3%, respectively). When compared with the Correlative SDM, the potential presence areas suggested by the Hybrid approach for the current climate were almost the same for the American continent (compare Figure 2b,h) resulting in a similar Sensitivity (Table 1). On the other hand, larger presence areas were projected by the Hybrid SDM for the westernmost coasts of Africa and the Canary Islands, suggesting in these coast temperatures within the physiological

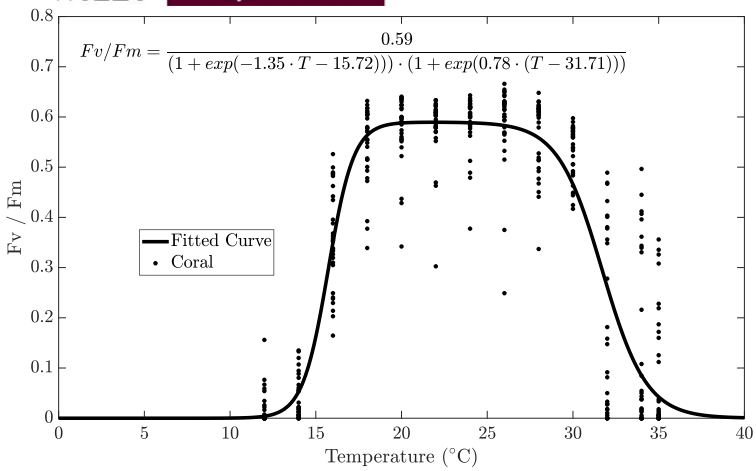

FIGURE 3 Response curve of the Maximal Quantum Yield of Photosynthesis (*Fv*/*Fm*) of *M. alcicornis* with temperature. The points indicate the *Fv*/*Fm* measurements for each coral fragment (n = 30) using a Pulse Amplification Fluorometer (PAM). The line represents the fitted curve: $Fv/Fm = a/((1 + \exp(-b*(T-c)))*(1 + \exp(d*(T-e))))$ (R^2 = 0.82), where T represents the temperature, and the coefficients (95% confidence intervals) are as follows: a = 0.5899 (0.5719, 0.6078), b = 1.346 (0.9843, 1.707), c = 15.72 (15.53, 15.91), d = 0.7756 (0.6392, 0.9119) and e = 31.71 (31.43, 31.98)

tolerance of the species detected in the experiment and incorporated in the model. In discrepancy with the Physiological model, but analogous to the Correlative SDM, the 'Hybrid map' showed discontinued absences in areas of low salinity overlapping with the Mississippi, Amazon, Niger, and Congo rivers. It incorporated the restriction to low salinity captured by the correlative approach, and thus Specificity was similar between these two models, and higher than that of the Physiological model (Table 1).

For the future A2 scenario, 35.7% of the territory was estimated as presence area (Table S3). There were increases of new potential presence areas respect the current projections (12.0%, Table S3) on the inner eastern coasts of the USA, Guyana, Surinam, the northern coasts of Spain and Portugal, and the coasts of Senegal, Guinea and Namibia (Fig. 2i). Tenerife still maintained the potential probability of presence in 2100, comparable to the expansion forecasted by the Correlative SDM (compare Figs. 2c & i). Remarkably, potential new absence areas, mostly not captured by the Correlative SDM, expanded along the Caribbean Sea, Brazil, and a small spot by Sierra Leone, in response to predicted increases in seawater temperatures exceeding the species physiological threshold (Figs. 2h, i). This resulted in an increase of 3.2% of new absence areas compared with the current projections and a sum of 64.3% of total absence areas for the year 2100 (Table S3).

3.4 | Models evaluation in current scenarios

Overall, all models correctly classified the current presence areas of *M. alcicornis*, which mostly extend along the tropical western Atlantic, thus showing high Sensitivity values (Table 1). However, models performed differently in classifying the absence areas of the species (mostly along the African coasts). The Physiological model based on the thermal threshold was different than the other two in classifying most of the territory of higher suitability from the present-day climatic conditions onwards, and thus was of poor Specificity and of high Commission error respect to the other two (Table 1).

The evaluation metrics for the two SDMs fitted with MaxEnt and based on random internal partitioning of presences (70:30), ranked the Correlative SDM somewhat better than the Hybrid in discriminating presence and absence areas by both the mean regularized training gain and AUC metrics (Table 1), although all values were indicative of correct model performance. On the contrary, the geographic transferability validation presented higher values of AUC for the Hybrid SDM (0.95) than for the Correlative SDM (0.85), as well as for the regularized training gain (0.63 and 0.37, respectively, Table 1), thus suggesting its better performance when the partitioning is done by a geographic criterion.

3.5 | Comparisons of predictions

Projected future environmental conditions largely exceed those in the training data (Sstmean > 31.5°C and Salinity > 37.3 PSS) for the three IPCC scenarios and thus extrapolations from independent models resulted in different predictions. The Correlative SDM extrapolated high suitability continuously to the maximum value set by the truncated response curve (mean temperatures > 31.5°C were extrapolated to suitability values of 0.71, Fig. S1). This is unrealistic because experimental results suggest decreased hydrocoral physiological performance at temperatures above 32°C (Fig. 3). This was captured by the Hybrid and Physiological models when predicting large absences at the central distribution of the species in the future. Nevertheless, the Hybrid SDM also included the constraint by low salinity suggested by the distributional records, thereby allowing it to predict absences in river mouths outperforming the Physiological model (Fig. 2i).

Regarding spatial bias in future projections, the MoD figure obtained by the Hybrid SDM (Fig. 4b) indicated a smaller area of uncertainty in comparison to the Correlative SDM associated only with salinity values outside the training data (Fig. 4a). In the

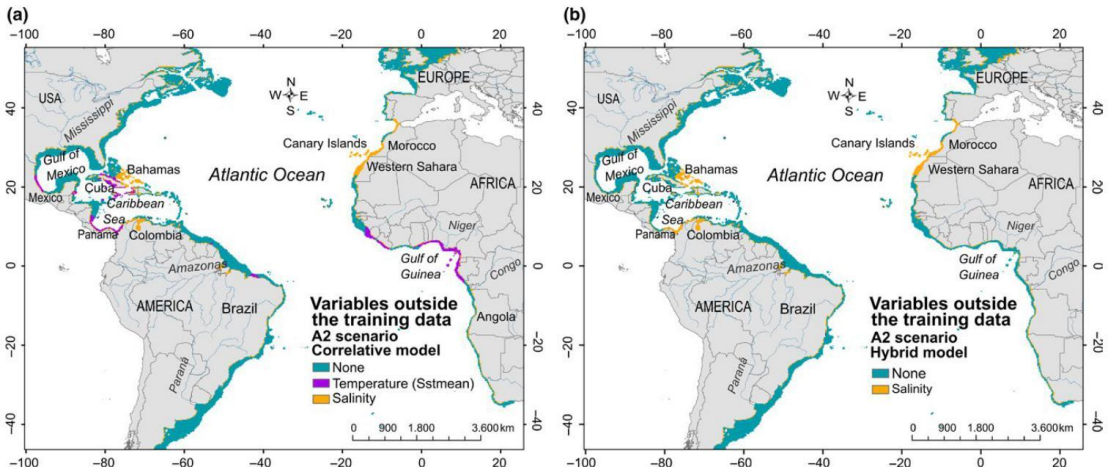

FIGURE 4 Most dissimilar variable (MoD) areas in the Atlantic Ocean where environmental predictors are extrapolated outside the training data when applying the A2 future climatic scenario to the distribution of *M. alcicornis*. Colours indicate the variable furthest outside the training range in (a) the Correlative model and (b) the Hybrid model. Extrapolations in Sstmean (in purple) extend along Cuba, Panama and Gulf of Guinea with the Correlative model. Under both models, extrapolations of Salinity (in orange) affect mostly the Bahamas, Colombia, Canary Islands and Morocco. Turquoise represents the areas not affected by variables outside the training data

Hybrid SDM, future non-analogous areas for the physio-climatic variable were null because the physiological response function was bell-shaped, and therefore, low values of the *Fv/Fm* ratio were achieved for two (cold and warm) current thermal conditions. Hence, the Hybrid model was trained at all possible values of *Fv/Fm* avoiding extrapolations in future climate scenarios (see the double scale on the right panel in Supporting Information Figure S1b). In summary, by reducing extrapolation, the Hybrid SDM suggested current unoccupied potential presence areas (e.g., Western Sahara and Angola), and possible future areas of absence not detected by the Correlative SDM (e.g., Cuba, Mexico or Gulf of Guinea), as it also captured the correlative information on Salinity unnoticed by the Physiological model.

4 | DISCUSSION

We provide in this study an improved and transferable method to predict distributional shifts of species in future environmental conditions that do not currently exist. This was achieved by integrating physiological knowledge into correlative SDMs to develop Hybrid SDMs, following the idea of using the output layers of a mechanistic model as the input layers for a correlative one (Buckley et al., 2011; Elith et al., 2010; Mathewson et al., 2016). We defined a physio-climatic predictor of thermal tolerance for the fire coral in each location by relating the thermal conditions at these sites, with the potential photosynthetic performance of its symbionts observed in experiments, which is closely related to their survival. This physio-climatic variable can be viewed as a transformation of the temperature layer into a meaningful raster for the physiology and survival of the coral. Moreover, as this variable was an adequate predictor of habitat suitability, MaxEnt and other common modelling algorithms selected it as a major predictor for the Hybrid SDMs. Similar to the Correlative SDM, the Hybrid SDM also accounted for other important physi-cal drivers (salinity in this study), as captured by the correlations between presence records and environmental layers. Although the Hybrid SDM did not outperform the Correlative SDM when the in-ternal validation was applied to current climatic conditions, it did so in the geographic transferability assessment, and provided robust predictions for future climatic scenarios by reducing the areas of extrapolation to non-analogous climatic conditions. This is particularly interesting when forecasting the future fate of foundational cor-als and other tropical organisms, which are expected to withstand higher temperatures than current ones.

To build a Hybrid SDM, a physio-climatic variable can be defined and included as a predictor in the SDM (this study; Elith et al., 2010). This physio-climatic predictor should be a direct estimator of the survival of the species under a limiting environmental factor. If this is not possible, a physiological proxy of the organism's performance may be used, for example, oxygen consumption that assesses the metabolic rate in fishes (Cech & Brauner, 2011), net assimilation rates that indicate plant growth (Williams, 1946) or the *Fv/Fm* to as-sess the photosynthesis yield in photosynthetic organisms, as in this study (Maxwell & Johnson, 2000). This information can be obtained from previous ecophysiological studies, as summarized in new da-tabases (e.g., Bennett et al., 2018). However, the description of the physiological response at all range of environmental conditions, that is, the bell-shaped double-logistic regression, is often unavailable, and its variation due to phenotypic plasticity and/or local adapta-tion is usually unknown (Valladares et al., 2014). After obtaining the

response function from literature or using experiments, it is applied to each pixel of the physical raster layer (Sstmean in this study) to obtain the physio-climatic predictor (Yieldsstmean). This new physio-climatic raster encompasses all the possible values of the variable because functions of vital traits are bell-shaped; therefore, the low values will result either from low or high physical conditions, whereas high values will result from optimum conditions. This allows training the Hybrid SDM in all possible values of the physio-climatic predictor, and therefore, extrapolations in this variable on projec-tions are avoided. In this study, the low values of *Fv*/*Fm* expected for future warming scenarios were related to low habitat suitability by both too cold and too warm temperatures for the occurrence of the coral in the current climate. Finally, additional physical predictors (e.g., Salinity) can also be included into the Hybrid model, and then fitted and validated following standard procedures.

Hybrid SDMs can be readily applied to marine organisms with geographic ranges that typically conform better to their thermal physiological thresholds than terrestrial species (Sunday, Bates, & Dulvy, 2012). In addition, as the ocean temperature does not show large oscillations compared to atmospheric temperature (Kearney & Porter, 2009; Martínez et al., 2015), physiological information is easier to relate to averaged environmental data from satellite imagery (Smale

& Wernberg, 2009). However, we do not exclude its generalization to terrestrial systems as environmental rasters are gaining meaning with respect to the physiology of organisms (Assis et al., 2018; Kearney, Isaac, & Porter, 2014). Similar approaches to improve SDMs predic-tions have been developed by several authors; for example, Elith et al. (2010) with toads, combining climatic variables and the output of a mechanistic model (Kearney et al., 2008). Also Buckley et al. (2011) with butterflies, using a predictor based on their lower developmen-tal time. And Mathewson et al. (2016) that predicted the distribution of a terrestrial endotherm incorporating its predicted surface-activity time, obtained from Niche Mapper, into a SDM, to conveniently proj-ect the spatial variation of the species' thermoregulation response to future warming scenarios. The main difference of our proposed Hybrid SDM with these studies is that while they use mechanistic models based on modelling platforms, ours is based on empirical re-sults which are direct measures of the organism' physiology.

When comparing the Physiological, Correlative and Hybrid models to determine the best option for predicting the geographic distribution of *M. alcicornis*, the Hybrid SDM had the best perfor-mance and overcame the disadvantages of the other two methods. The Physiological model clearly overestimated the presence areas, classifying in the current climate, the entire American and African coast from 40°N to 40°S as of presence, and omitting the absence areas in river mouths. This model represented well the potential thermal niche (sensu Jackson, Overpeck, Paleobiology, & Autumn, 2000), that is, the portion of the fundamental niche existing in the geographic space, but without considering other niche axes, resulted in the overestimation of the habitat (Martínez et al., 2015). The in-clusion of other environmental constraints in the Hybrid SDM by in-corporating the relationship with salinity (as in the correlative SDM) partially solved this restriction. This model projected a more realistic expansion of *M. alcicornis* in regions of the African coast, according to the recent evidence of establishment of populations at higher lati-tudes in the Canary Islands (Clemente et al., 2010). It also accounted for the limits of the potential niche of thermal tolerance, which re-sulted in novel predictions of decline in the centre of distribution that were unnoticed by the extrapolations of the correlative SDM. This prediction is in concordance with the trend observed by tropi-cal corals worldwide (see Section 1). In this way, hybrid models can help establish priority conservation areas in regions that would not be detected with correlated models, which represents an important tool for early warning systems (Keith et al., 2014).

The future projections of climatic conditions included values out-side current levels, which will become common for corals, as they are tropical organisms living close to the hottest temperatures found in the ocean. As aforementioned, the Hybrid SDM reduced the uncer-tainty associated with future extrapolations. Descombes et al. (2015) solved the problem of inferring extrapolations by using Eocene coral fossil data and the corresponding climatic conditions (warmer than the IPPC scenarios) to describe the whole thermal response curve for corals, assuming that the fossil records correctly captured the entire environmental range limits of the species. However, if the fos-sil record is incomplete, and/or represents an unfilled niche, then our proposed Hybrid SDM can overcome these problems because it uses the fundamental thermal niche of ecophysiological tolerance. Anderson (2013) proposed this solution when the niche space as-sumption is violated, that is, when the study does not contain the full range of conditions that a species tolerates, and thus, the response curves are truncated. The results obtained with the Hybrid SDM showed a future decline in the areas where future temperatures will exceed the physiological thermal threshold of this species. At pres-ent, there is no similar mechanistic knowledge about Salinity, but it can be easily incorporated from additional experiments using our hy-brid approach, as well as other relevant physio-climatic variables and emerging physiological knowledge.

According to Carpenter et al. (2008), corals are at higher risk of extinction due to climate change, where recurrent bleaching events are linked to the increase in sea surface temperatures (Hoegh-Guldberg, 1999), for example, a catastrophic event affected the Great Barrier Reef during 2016 (Hughes et al., 2016). The most feasible measure of bleaching is the photosynthetic efficiency (*Fv*/*Fm*), which is con-sidered a good indicator of coral health (Roth, 2014). Under labora-tory conditions, we found that *M. alcicornis* exhibited a suboptimal decrease in *Fv*/*Fm* and degraded health at temperatures below 16°C and above 32°C. Future projections under the A2 scenario indicate temperature increases that would exceed the physiological upper thermal tolerance limit for this species, mainly in the Caribbean Sea and Gulf of Mexico. However, these regions were not projected as areas with declines in habitat suitability for coral reefs by other stud-ies based on SDMs using the same scenarios (see Couce, Ridgwell, & Hendy, 2013), which did not incorporated physiological knowledge. The upper thermal limits found in our study agreed with those that define potential areas of bleaching for scleractinian corals (Donner, Skirving, Little, Oppenheimer, & Hoegh-Gulberg, 2005), and with the

future hyper-tropical zone proposed by González-Duarte, Megina, López-González, and Galil, (2016), where mass mortalities are ex-pected. The projected areas of decline determined by our Hybrid SDM represented 2.5% of the current suitable areas (~1.63 × 10^7 ha). If these projections are met, assuming there is no time for thermal adaptation and accounting that the most pessimistic temperature scenario is being used in this study, these areas will lose a key reef- forming species, which may lead to reef degradation, and loss of ma-rine biodiversity and ecosystem services (Carpenter et al., 2008). The ability to detect areas potentially vulnerable to climate change, unde-tected by other methods, highlights again the importance of Hybrid SDMs as early warning tools for conservation management plans, for example, anticipating areas which need urgent conservation support (see Beger, Sommer, Harrison, Smith, & Pandolfi, 2014).

On the other side, due to seawater temperature increases (as those projected by the A2 scenario), this study predicted *M. al-cicornis* spread to other subtropical and temperate areas of minimal temperature >16°C, if allowed by its dispersal capacity and biotic interactions. The current presence of *M. alcicornis* in the Canary is-land of Tenerife already supports this fact. López et al. (2015) es-tablished the genetic origin of *M. alcicornis* as the Caribbean region from where it could have been rafted by the Gulf Stream (López et al., 2015). *M. alcicornis* is a pioneer species, which can provide habitat for other associated marine biota, such as tropical fish (Coni et al., 2013), which have already appeared in Tenerife (see Brito, Falcón,

& Herrera, 2005), thereby indicating a potential tropicalization of this Archipelago. Poleward range expansions of tropical corals have already been reported worldwide (Greenstein & Pandolfi, 2008; Yamano et al., 2011), and although they may serve as a refuge against climate change effects, they could also cause ecological problems by out-competing native species that are currently in decline such as their temperate counterparts the macroalgae (Serrano, Coma, & Ribes, 2012; Vergés et al., 2014; Wernberg et al., 2016).

In summary, the potential distribution of *M. alcicornis* will ex-pand to higher latitudes by the year 2100 and experience contrac-tions in some tropical regions due to climate change. As suggested by Elith et al., (2010) and Buckley et al. (2011), and corroborated in this study, it is feasible to develop Hybrid SDMs integrating physiological knowledge into correlative SDMs. The reliability of future predictions is improved because this mechanistic knowl-edge encompasses the entire range of physiological response for the species, and thus, extrapolation is reduced. They can be used for detecting potential areas of extinction or invasion, assessing the potential effects of climate change on biodiversity (Pearson

& Dawson, 2003) and guiding conservation actions. Despite all the limitations due to the inherent complexity of natural systems, Hybrid SDMs can be useful tools to assess the potential effects of climate change on biogeographic patterns.

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BIOSKETCH

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Author contributions: L.R. and B.M. conceived the ideas; L.R. and J.J.G. collected the data; L.R. led the literature search, analy-sis and writing; and all authors were involved in revising of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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CHAPTER 5

Genetic relationships of the hydrocoral *Millepora alcicornis* and its symbionts within and between locations across the Atlantic

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REPORT

Genetic relationships of the hydrocoral Millepora alcicornis and its symbionts within and between locations across the Atlantic

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Abstract Although the hydrocoral Millepora alcicornis is a prominent and ecologically relevant amphi-Atlantic reef builder, little attention has been given to its endosymbionts which are also involved in the survival and adaptation success of the species in different environments. In this study, we resolve the genetic relationships between M. alcicornis and its symbionts (Symbiodiniaceae) within both sides and across the Atlantic. The COI and 16S-rDNA regions were selected for the host tissues, and the 23S-rDNA and ITS regions were chosen for the symbionts. Phylogenetic networks consistently showed that host pop-ulations from the eastern Atlantic archipelagos (Canary and Cape Verde Islands) were more related to western Atlantic populations than they were between them. However, results for Symbiodiniaceae species varied according to the molecular marker used. Samples from Mexico were grouped as Symbiodinium sp. (formerly Symbiodinium clade A) by both markers. Specimens from Puerto Rico were grouped as either Symbiodinium sp. or Breviolum sp. (formerly Symbiodinium clade B), according to the molecular marker used. Most samples from the eastern Atlantic were identified as Breviolum sp. by both markers, except for one sample from the Canary Islands and two samples from the Cape Verde Islands, which were identified as Cladocopium sp. (formerly Symbiodinium clade C) using ITS-rDNA. These results suggest that these two genera of Symbiodiniaceae may cohabit the same M. alcicornis colony. Because hydrocorals from the Canary Islands were phylogenetically related to the western Atlantic, but symbionts were more related to those of the Cape Verde Islands, the origin of the coral and its symbionts is probably different. This may be explained either by ''horizontal'' transmission, i.e. acquisition from the environment, or by a change in the dominant symbiont composition within the host. The flexibility of this hydrocoral to select symbionts, depending on environmental conditions, can provide new insight to understand how this coral may face ongoing climate change.

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Introduction

Coral reefs are among the most biologically diverse and economically important marine ecosystems, providing vital services to humans, including fisheries, coastal protection, medicines and tourism activities (Hoegh-Guldberg et al. 2007; Srividhya and Chellaram 2012). The main reef framework is typically built by calcifying corals (phylum Cnidaria), such as scleractinians and hydrocorals (Buddemeier et al. 2004). Their three-dimensional structure provides multiple microhabitats, leading to a great diversity and abundance of associated organisms (Graham and Nash 2013). Many corals host photosynthetic symbionts, i.e. dinoflagellates, belonging to the family Symbiodiniaceae (LaJeunesse et al. 2018). This association is of fundamental ecological importance, the host provides inorganic nutrients and refuge from herbivory to its symbionts and, in turn, the symbionts contribute to host nutrition by provid-ing photosynthetically fixed carbon and enhancing coral skeletogenesis and reef development (Weis et al. 2001; Yellowlees et al. 2008; Davy et al. 2012).

Symbiotic hydrocorals of the genus *Millepora* are important reef builders, covering extensive areas in shallow tropical reefs around the world (Boschma 1948; de Weerdt 1984). They are commonly found in both the Indo-Pacific and Atlantic Oceans (Razak and Hoeksema 2003; Amaral et al. 2008; Ruiz-Ramos et al. 2014, Takama et al. 2018). In the Atlantic, most *Millepora* species inhabit the western basin (Caribbean and Brazilian biogeographic provinces), with the exception of *Millepora alcicornis* (Linnaeus 1758), which has an amphi-Atlantic distribution as evidenced by its presence in the Cape Verde Islands (Laborel 1974), Ascension Island (Hoeksema et al. 2017) and the Canary Islands (Clemente et al. 2010). Asexual reproduction by fragmentation is the main mechanism to form new zooids of *M. alcicornis*, because they breed infrequently, releasing sexual medusae seasonally (Lewis 1989, 2006). This hydrocoral has high growth and recruitment rates (Lewis 2006) and is capable of colonizing both natural and artificial substrates, from dead gorgonians and rocks to the hull of ships (Bertelsen and Ussing 1936; Wahle 1980). This ability to inhabit different substrates and its rapid colonization rates (Clemente et al. 2010) provide a competitive advantage for potential habitat expansions.

Symbiotic dinoflagellates of the family Symbiodiniaceae live in association with *Millepora* spp. (van Oppen et al. 2009). Recently, the differentiation of 7 genera (previously referred to as clades of *Symbiodinium* spp.) has been described for the family Symbiodiniaceae (LaJeunesse et al. 2018). Some symbiont genera are widely distributed across extensive oceanographic regions and at different depths (Baker 2003; Rodriguez-Lanetty and Hoegh-Guldberg 2003). Others have narrow geographic distributions, e.g. Temperate "Clade A" (previously termed S*ymbiodinium* "Temperate A"), mainly found in the Mediterranean (Visram et al. 2006; Casado-Amezúa et al. 2016). Some corals present high levels of symbiont specificity, e.g. *Acropora palmata* with *Symbiodinium* "*fitti*", nomen nudum (A3) (Pinzón et al. 2011), while others can host several Symbiodiniaceae genera within the same colony (Rowan and Knowlton 1995; Apprill and Gates 2007; Kemp et al. 2015; Grajales and Sanchez 2016). Symbiont acquisition differs among corals. Some transmit their symbionts directly to their offspring (vertical transmission), ensuring the viability of the juvenile coral. Other species acquire symbionts from the environment (horizontal transmission) through phagocytosis of symbionts (Hirose et al. 2001; Weis et al. 2001; Stat et al. 2006, 2008) expelled from other hosts, such as corals, molluscs, foraminifera, anemones (Rodriguez-Lanetty 2003), flatworms (Kunihiro and Reimer 2018), or they may uptake free-living symbionts (e.g. Reimer et al. 2010b; Nitschke et al. 2016). Others utilize both strategies, acquiring physiologically advantageous novel symbionts through horizontal transmission, which are perpetuated via vertical transmission (Byler et al. 2013). When corals suffer stressful conditions, some of them can replace their symbionts, via horizontal transmission, with other "host-compatible" symbionts. However, once the stressful situation is over, they usually recover their original symbiont species (Sampayo et al. 2016), reducing the stability of the new symbiotic association over the long term (Coffroth et al. 2010; Sampayo et al. 2016). Others can also change their internal abundance and composition of symbionts under adverse conditions (Berkelmans and van Oppen 2006), or even seasonally (Gates 1990; Yang et al. 2000; Warner et al. 2002; Costa et al. 2013). Other species do not change their symbionts under stressful conditions (Goulet 2006, 2007).

The ancient association complex of Cnidaria–Symbiodiniaceae is extremely diverse and provides multiple functional traits for the holobiont as a whole (e.g. Mieog et al. 2009; LaJeunesse et al. 2018). For example, the thermal tolerance of some corals may depend on the Symbiodiniaceae species that it hosts, while the physiological response of the symbiont may depend on the host population origin, or its genetic background (Mieog et al. 2009; Parkinson et al. 2015). Thus, the coral and its symbionts need to be considered as a single unit to better understand their biological and ecological responses to

environmental conditions, which is fundamental to predict how coral reefs will face climate change (Parkinson and Baums 2014; Grajales and Sanchez 2016).

Hydrocorals are sessile marine invertebrates, and their medusoid larval stage and asexual fragments represent their opportunity for dispersal (Lewis 2006; Ortiz-González et al. 2017); however, they are difficult to track. Molecular tools provide an ideal technique for an indirect assessment of their phylogenetic relationships, connectivity and population structure (Hunter et al. 1997; Van Oppen et al. 2001; Vollmer and Palumbi 2004). Govindarajan et al. (2005) suggested that the cytochrome oxidase subunit I (COI) and the 16S-rDNA are useful molecular markers for hydrozoan phylogeographic studies. Zheng et al. (2014) recommended the use of 16S-rDNA for DNA barcoding and phylogenetic analyses of hydrozoans at the genus level. Both markers demonstrated high genetic diversity for *Millepora* spp. in the Caribbean Sea, which are the source populations of the eastern Atlantic *M. alcicornis* found in the Cape Verde and Canary Islands (López et al. 2015; de Souza et al. 2017). Most of the studies based on symbiont identification point towards the use of multiple markers (e.g. LaJeunesse et al. 2012). For example, Santos et al. (2002) used the chloroplast large-subunit 23S-rDNA to infer its molecular phylogeny. LaJeunesse (2001) used the internal transcribed spacer (ITS) region for the same purpose and to investigate the biodiversity and ecology of the symbionts. Santos et al. (2001) also used the ITS for comparing cultured *versus* freshly isolated zooxanthellae, detecting that a single host can contain heterogeneous symbiont populations. Within those, the ITS region is often analysed to differentiate genera in the family Symbiodiniaceae (Coffroth and Santos 2005; LaJeunesse et al. 2010, 2012, 2018). In particular, the ITS2 region has been used to resolve symbiont diversity at the classical subclade level (LaJeunesse 2001; LaJeunesse et al. 2004; Sampayo et al. 2009; Stat et al. 2011; Arif et al. 2014). Despite the abundant scientific literature based on genetic analyses of corals or symbionts, only a few studies have combined genetic analyses of both components of the Cnidaria–Symbiodiniaceae association, e.g. Alcyonacea–Symbiodiniaceae (Coffroth et al. 2001), Actiniaria–Symbiodiniaceae (Thornhill et al. 2013), Zoantharia–Symbiodiniaceae (Reimer et al. 2010a, 2017) and Scleractinia–Symbiodiniaceae (Thornhill et al. 2006; Mieog et al. 2009; Pettay et al. 2011; Casado-Amezu´a et al. 2014; Shinzato et al. 2014; Picciani et al. 2016).

To date, three studies have analysed the genetic structure of *M. alcicornis* across the Atlantic (López et al. 2015; Hoeksema et al. 2017; de Souza et al. 2017). However, all of them have only considered the host and have employed analyses based on a single gene, without including their endosymbionts in the analyses. Including symbionts in the analyses could improve the resolution for delineating the genetic structure of the hydrocoral–symbiont association. In this study, we used four molecular markers, two for *M. alcicornis* (COI and 16S-rDNA) and two for its symbionts (23S-rDNA and ITS-rDNA), with the aim of resolving the genetic relationships for the hydrocoral–Symbiodiniaceae association within and between populations from across the Atlantic. This combined analysis (host and symbiont) might help to understand the origin and colonization process of this holobiont into new regions, such as the Canary Islands, and how it may respond to varying environments. This information might be relevant when evaluating possible global warming scenarios that may result in shifts in species distribution towards the eastern Atlantic (e.g. González-Delgado et al. 2018).

Materials and methods

Sample collection

A total of 62 fragments of *M. alcicornis* were collected by scuba diving or snorkelling, between the intertidal zone down to 14 m depth (Table S1) at 15 sites across the Atlantic (Fig. 1). The corresponding national permits were obtained when needed (e.g. Mexico, Conapesca 01-013). All samples were preserved in dimethyl sulfoxide (DMSO) until further analyses.

DNA extraction and PCR conditions

DNA from 50 mg of tissue, scraped from each specimen, was extracted using the DNeasy Blood & Tissue Kit (Qiagen®, Redwood City, CA, USA), following the manufacturer's instructions. The polymerase chain reaction (PCR) was used to amplify two fragment genes from the host tissue (COI and 16S-rDNA) and from their Symbiodiniaceae symbionts (23S-rDNA and ITS-rDNA). PCR amplifications were performed in a total volume of 25 µl, containing 1X buffer (GeneAll Biotechnology, South Korea), 0.2 mM of each dNTP, 0.4 µM of each primer, 1U of Taq DNA polymerase (GeneAll Biotechnology, South Korea) and 20 ng of total genomic DNA.

PCR cycle conditions consisted of an initial cycle at 94 °C for 2 min, followed by 40 cycles at 94 °C for 10 s, an annealing temperature specific to each primer (see Table 1) during 20 s, and 30 s at 72 °C, with a final extension at 72 LC for 10 min. Amplified products were checked by 1% agarose gel electrophoresis and, subsequently, the unincorporated primers and nucleotides were removed with the ExoSAP-IT kit (GE Healthcare Illustra, Sweden). Finally, the samples were sequenced by the Genomic Service (SEGAI) of the University of La Laguna.

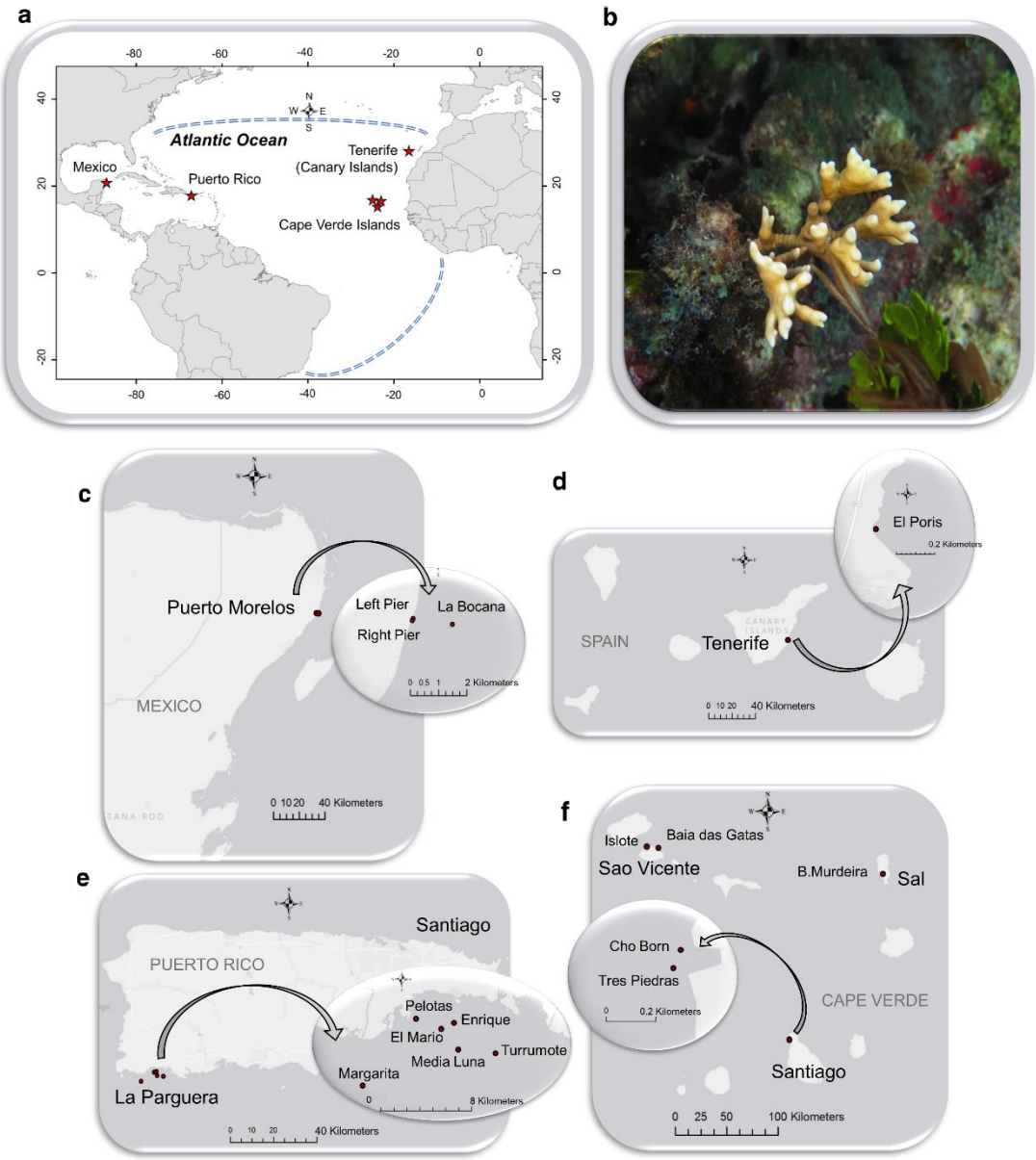


Fig. 1 **a** Map denoting sample collection sites in the Atlantic Ocean (red stars). Limits of the current distribution of *Millepora alcicornis* are included by double dashed blue lines. **b** *M. alcicornis* from La Bocana (Mexico). Photograph credit: Laura Rodríguez. Sample sites in **c** Mexico, **d** Spain (Tenerife), **e** Puerto Rico and **f** Cape Verde Islands

The sequences obtained in this study were deposited in GenBank (see accession numbers in Table S1).

Sequence editing, alignment and analysis

DNA sequences were edited and assembled using MEGA7: Molecular Evolutionary Genetic Analysis, version 7.0 (Kumar et al. 2016). Sequence alignments were performed

Table 1 Summary of the organisms and primers used for genetic analyses

Organism	Region	Primer	Primer sequence	Size (bp)	Ta (°C)	Substitution model	References
Millepora alcicornis	COI (mitochondrial)	COIF	5′TAG-AAT-TAG-CTG-GGC-CAG-GA-3′	462	50	–	Modified from Ruiz-Ramos 2009 MMX: PureTaq Ready-To-Go PCRbeads (GE Healthcare, Uppsala, Sweden)
		COIR	5′CCT-GTC-TGT-AAG-CAG-CAT-GG-3′				
Millepora alcicornis	16S-rDNA (mitochondrial)	16SAR	5-TCGACTGTTTACCAAAAACATAGC-3	469	52	–	Cunningham and Buss (1993)
		16SBR	5-ACGGAATGAACTCAAATCATGTAAG-3				Modified from Santos et al. (2001)
Symbiodinium sp.	23S-rDNA (plasmid)	23S2M13	5-CACGACGTTGTAAAACGACGGCTG TAACTATAACGGTCC-3	514	51	GTR + G	Santos et al. (2002)
		23S2M13	5-GGATAACAATTTCACACAGGCCA TCGTATTGAACCCAGC-3				
Symbiodinium sp.	ITS (nuclear)	ZITSUPM13	5-CACGACGTTGTAAAACGACCCGGTG AATTATTCGG ACTGACGCAGTGCT-3	638	55	GRT + I+ G	Modified from Santos et al. (2002) MMX: PureTaq Ready-To-Go PCRbeads (GEHealthcare, Uppsala, Sweden)
		ZITSDNM13	5-GGATAACAATTTCACACAGG CTGTTTA GTTCCTTTTCCTCCGC-3				

Substitution model obtained from the *J*ModelTest used in MRBAYES to construct the phylogenetic analyses of the symbiont samples

Bp base pair, *Ta* annealing temperature

using CLUSTAL W (Thompson et al. 1994), as implemented in MEGA7, and further revised by eye. In all cases, both sequence ends were trimmed manually to remove low-quality regions. Additionally, a total of 81 sequences of COI and 28 sequences of 16S-rDNA from the Car-ibbean, the coast of Brazil and the central Atlantic were obtained from GenBank to complete a representative sample size of *M. alcicornis* across the Atlantic. Network 5.0.0.3 software (Fluxus Technology©, www.fluxus-engi neering.com) was used to generate one haplotype network for each marker.

Poorly aligned regions from the alignment of 23S-rDNA and ITS-rDNA fragment genes from Symbiodiniaceae were removed using Gblocks® (Integrated DNA Technologies, Inc) (Castresana 2000). GenBank Symbiodini-aceae sequences for these genes (11 for the 23S-rDNA and 13 for the ITS-rDNA) defining the classical clades (A, B, C, D, E, F and G) were added to the analyses. The best-fitting DNA substitution model for each Symbiodiniaceae data set was determined according to the Bayesian infor-mation criterion (Schwarz 1978) in *j*ModelTest (Darriba et al. 2012) (Table 1). Phylogenetic trees of the symbiont samples were inferred using MrBayes 3.2.6 (Ronquist et al. 2012). The Markov chain Monte Carlo (MCMCs) were run for 5,000,000 generations and sampled every 100 genera-tions. Two independent analyses were run, and the simi-larity of the tree sample diagnostics was calculated every 100 generations. We left the default setting of MrBayes, which discards the first 25% samples from the cold chain, to obtain values of the potential scale reduction factor (PSRF) close to 1. Consensus trees were visualized through Fig.Tree v1.4.2 (Rambaut 2009). A suitable outgroup (*Gymnodinium* sp.) to each alignment was added to root the phylogram and identify the correct evolutionary pathway. To assess topological congruences between the 23S-rDNA and the ITS-rDNA phylogenetic trees, the congruence index (Icong) and its associated *p* value were calculated through the online programme http://max2.ese.u-psud.fr/bases/upresa/pages/devienne/index.help.html (de Vienne et al. 2007).

To identify the correspondent species (formerly sub-clades) hosted by each population of *M. alcicornis*, we analysed the ITS2 region. Once the genera hosted by each population were defined, independent phylogenetic trees were constructed for each genus: *Symbiodinium* (A), *Breviolum* (B) and *Cladocopium* (C), including sequences (subclades) from GenBank. The same methodology used for the analyses of ITS-rDNA and 23S-rDNA was followed for the ITS2.

Finally, restriction fragment length polymorphism (RFLP) analyses were developed following LaJeunesse and Trench (2000) to detect if two or more symbiont genera were cohabiting within the same *M. alcicornis* colony. Briefly, large-subunit RNA (hereafter LSUrDNA) was amplified following the conditions and primers described by Wilcox (1998) and PCR products were verified by agarose gel electrophoresis. Subsequently, amplification products were digested using Dpn II (New England Biolabs, USA), following the manufacturer's protocol, and products were visualized in an agarose gel (2%) stained with GelRed. The restriction digests of LSUrDNA were performed only for a subset of samples from Mexico (samples 1R, 1M, 1Ds, 2R, 2P and 4Ds), the Cape Verde Islands (samples CV5, CV15, CV18, CV20 and CV50) and Tenerife (samples CN21 and CN22).

Results

Millepora alcicornis genetic analyses

From the 134 sequences analysed for the COI fragment, 53 from this research (Table S1) and 81 obtained from GenBank (Table S2), a total of 89 haplotypes were obtained: 79 belonged to the Caribbean Sea, one to the Canary Islands, and nine to the Cape Verde Islands. Haplotypes from both eastern Atlantic archipelagos (the Canary and the Cape Verde Islands) were more related to the Caribbean than they were between them (Fig. 2a), with the most frequent haplotypes shared between the Caribbean and the Cape Verde Islands.

From the 74 sequences analysed for the 16S-rDNA region, 44 from our research (Table S1) and 30 from GenBank (Table S2), a total of 28 haplotypes were obtained: 14 from the Caribbean, one from the Canary Islands, nine from the Cape Verde Islands, three from Brazil and one from Ascension Island. The haplotype network for the 16S-rDNA fragment (Fig. 2b) confirms the results obtained for the COI region. Again, both eastern Atlantic archipelagos were more related to the western Atlantic than between them, and two haplotype groups were detected in the Cape Verde Islands. These two Cape Verde Islands haplotypes were more related to the western Atlantic than they were between them, with one of them also closely related to Ascension Island and distantly related to the Brazilian samples.

Symbiodiniaceae phylogenetic analyses

Symbiodiniaceae alignments contained 36 sequences for the ITS-rDNA, 23 from our study (Table S1) and 13 from GenBank (Table S2) representing all the existing genera described in the family. Symbiodiniaceae alignments also contained 45 sequences for the 23S-rDNA, 34 from our study (Table S1) and 11 from GenBank (Table S2). ITS-rDNA and 23S-rDNA analyses determined that different

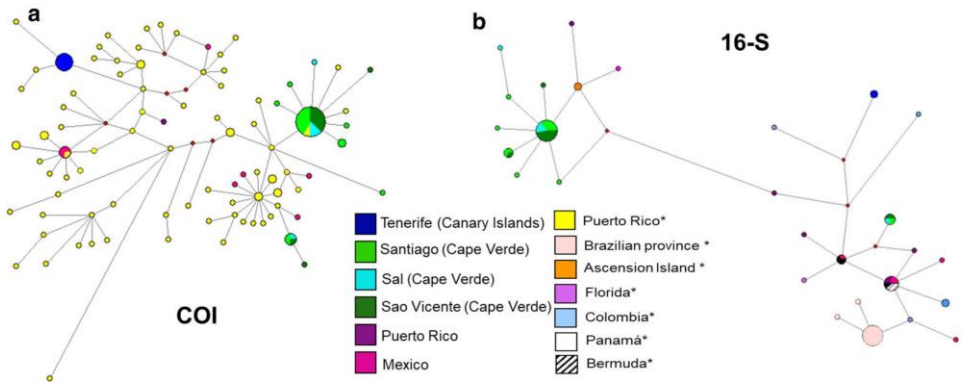


Fig. 2 Haplotype network based on a COI and b 16S-rDNA sequences of *Millepora alcicornis*. Additional GenBank sequences from those collected in this study were added to the network, e.g. western Atlantic and Ascension Island (Table S2)

Symbiodiniaceae genera are hosted by *M. alcicornis* (Fig. 3a, b, Table S1). The phylogenetic results of the ITS-rDNA (Fig. 3a) showed that all individuals from Mexico (representing 30.5% of the samples) hosted *Symbiodinium* sp. (formerly clade A) (Bayesian posterior probability, BPP = 1); in particular, type A4 as unveiled by the ITS2 analysis (Fig. S1b). Individuals from Puerto Rico, and most of the samples collected from the Cape Verde Islands (i.e. 56.5% of our samples), hosted *Breviolum* sp. (formerly clade B) (BPP = 1). The ITS2 phylogeny showed a high genetic diversity within this genus. Some individuals from the Cape Verde Islands (samples 5 and 7) grouped with type B23 and B30, while the rest of the samples were included within a group formed by types B1, B37, B10, B16, B17, B8 and B20 (Fig. S1a). Samples 20 and 18 from Santiago (Cape Verde Islands) and 21 from Tenerife (Ca-nary Islands) (i.e. 13% of the samples) hosted *Cladocopium* sp. (BPP = 1 (Fig. 3a), in particular type C1 as unveiled by the ITS2 analysis (Fig S1c).

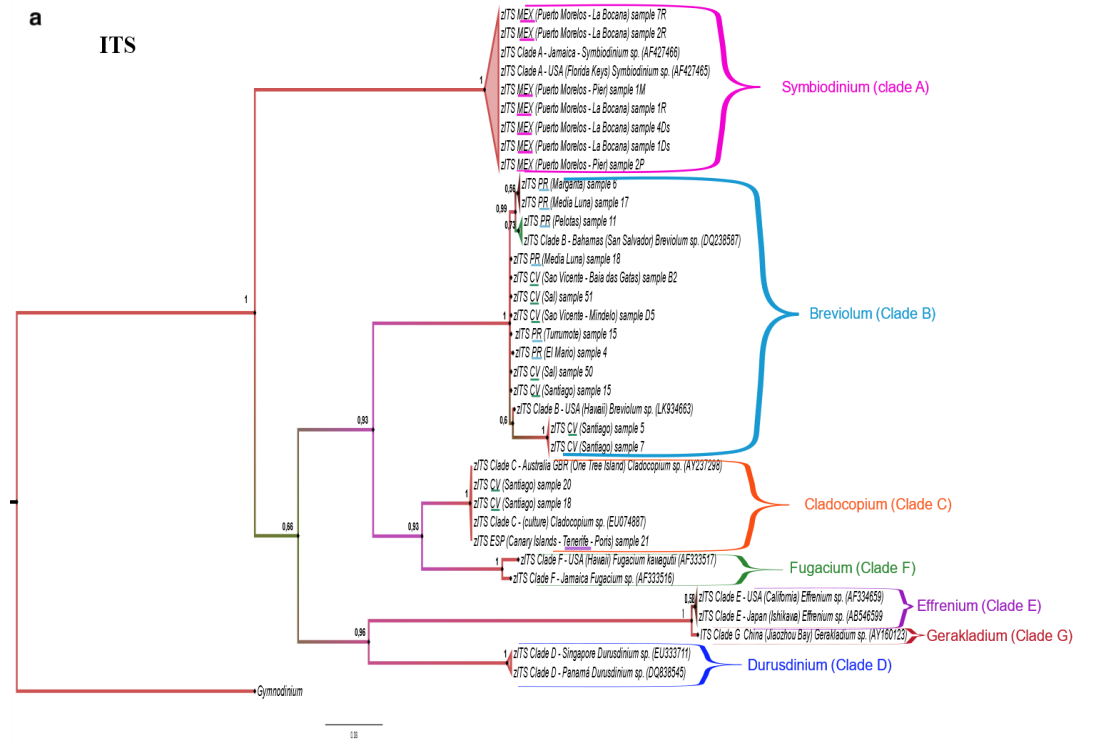
The 23S-rDNA (Fig. 3b) was able to separate two well-supported clades, grouping all samples from Mexico and Puerto Rico (Caribbean region), accounting for 41% of the samples, within *Symbiodinium* sp. (BPP = 0.91). The other group (BPP = 1) included all samples from the Cape Verde and Canary Islands, 59% of the samples, which fit with previously published sequences of *Breviolum* sp.

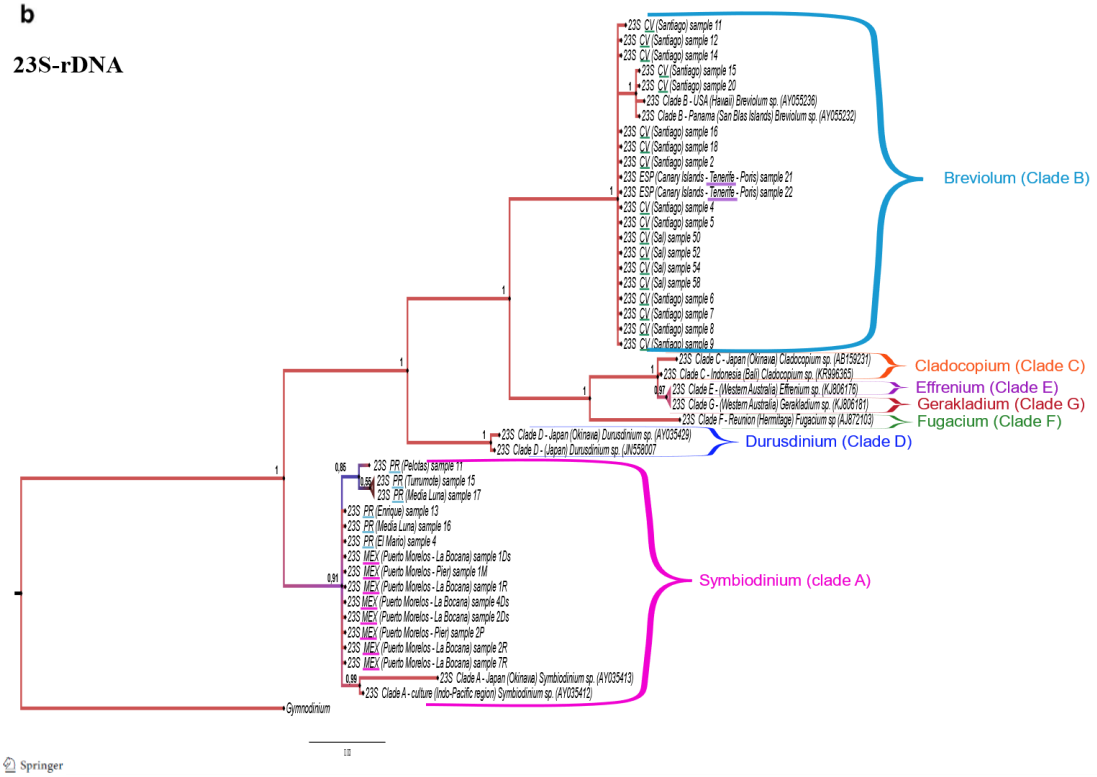
The LSUrDNA RFLP analyses indicated that samples from Mexico presented the same fragment pattern, showing two bands: one at 300 bp and another at 600 bp. All the Cape Verde Islands samples also presented the same band pattern among them (150 bp and 800 bp), indicating that all hosted the same symbiont type and different to those from Mexico. This outcome was congruent with the results of the phylogenetic trees. Regarding the two samples from Tenerife (Canary Islands), they presented the same band pattern as Cape Verde samples, but one of them also included an additional band. This fact may indicate the presence of more than one symbiont within the same host.

In summary, all the specimens from Mexico were found to contain *Symbiodinium* sp. for the two molecular markers, i.e. BPP [0.90 (Fig. 3a, b). Furthermore, we found that the Puerto Rico specimens were grouped within either *Symbiodinium* sp. and *Breviolum* sp., depending on the molecular region used, 23S-rDNA (BPP = 0.91) versus ITS (BPP = 1). Regarding the eastern Atlantic samples (Canary Islands and Cape Verde Islands), *Breviolum* sp. was the dominant genus when the phylogenetic tree was constructed with the 23S-rDNA marker (BPP = 1), while three sequences (one from Tenerife and two from Santiago) matched *Cladocopium* sp. according to the ITS-rDNA region (BPP = 1). In other words, *Cladocopium* sp. was only detected by the ITS region, in the eastern Atlantic specimens, from the recently established colonies of the Canary Islands, and in two of the nine samples from Cape Verde Islands (Fig. 3a, b). Meanwhile, the same samples matched with *Breviolum* sp. according to the 23S-rDNA region. Despite these differences, the congruence test value (Icong = 1.85) and its associated *p*-value of 4.5 9 10^{-5} indicated that the 23S-rDNA and the ITS trees were more congruent than expected by chance.

Differences between *Millepora alcicornis* and Symbiodiniaceae genetic analyses

The results extracted from the haplotype networks of the hydrocoral and the phylogenetic trees of its symbiont show different relationships among populations. While the analyses of the hydrocoral sequences confirm that samples from the Canary Islands are more related to the Caribbean than to those from the Cape Verde Islands, the


a
ITS
Symbiodinium (clade A)
Breviolum (Clade B)
Cladocopium (Clade C)
Fugacium (Clade F)
Effrenium (Clade E)
Gerakladium (Clade G)
Durusdinium (Clade D)
Gymnodinium


b
23S-rDNA
Breviolum (Clade B)
Cladocopium (Clade C)
Effrenium (Clade E)
Gerakladium (Clade G)
Fugacium (Clade F)
Durusdinium (Clade D)
Symbiodinium (clade A)
Gymnodinium

◄**Fig. 3** Phylogenetic analyses inferred from **a** ITS and **b** 23S-rDNA regions of *Symbiodinium* sp. hosted by *Millepora alcicornis* across the Atlantic: Mexico (Puerto Morelos, Puerto Rico, Cape Verde Islands, /Sal, Santiago, Sao Vicente) and Canary Islands (Tenerife)

the Symbiodiniaceae results indicate that the symbiont sequences from the Canary Island samples are more related to the Cape Verde Islands than the Caribbean. These results indicate that the origin of the hydrocoral, recently settled in the Canary Islands, and the origin of its symbionts are different.

Discussion

This is the first study focusing on the genetic relationships of both *M. alcicornis* and its symbionts within and across the Atlantic. Our results initially confirm the genetic variation of this hydrocoral and identifies the Caribbean as the region of origin for the recently established *M. alcicornis* colonies from the Canary Islands (López et al. 2015; de Souza et al. 2017) and provide further evidence for two independent founder events occurring in the Cape Verde Islands, previously reported by López et al. (2015). Importantly, we found a genetic mismatch between the hydrocoral-Symbiodiniaceae association, as the genetic relationships between both sides of the Atlantic varied between these two components. Hydrocoral haplotypes from the eastern Atlantic archipelagos (Canary Islands and Cape Verde Islands) were more related to the western Atlantic than they were between them, showing the same population structure previously found by López et al. (2015) and Souza et al. (2017). However, sequences of Symbiodiniaceae from the two eastern Atlantic archipelagos were considerably more similar than to those from the Caribbean. According to our results, the origin of the symbionts from the Canary Islands colonies did not follow the same pattern as the hydrocoral; probably due to acquisition of the symbionts from the environment, or because changes in the internal symbiont abundances have taken place in colonies from the Canary Islands.

Millepora alcicornis has two free living stages during sexual reproduction, a jellyfish and a fertilised planula larva to further disperse the species (Lewis 2006). However, the period of time they spend in the water column is short, impeding long distance dispersion (Hickson 1899; Mayer 1910; Weerdt and Glynn 1990; de Souza et al. 2017). Therefore, the success of *M. alcicornis* resides in asexual reproduction by small fragments, which are able to travel in ballast water, encrusted on the hull of ships, or on floating materials (López et al. 2015; de Souza et al. 2017). *Millepora alcicornis* arrived at the Canary Islands via the Gulf Stream (López et al. 2015), and we would expect that those colonies brought their symbionts with them; but our results suggest a shift in symbionts within the Canary Island population. *M. alcicornis* hosted different species within the Symbiodiniaceae across the Atlantic, without a congruent genetic pattern between the host and its symbiont. Specifically, eastern Atlantic Symbiodiniaceae populations seemed to be genetically related, in contrast to the pattern obtained for the hydrocoral. The topological congruence test between the chloroplast and the nuclear phylogenies of Symbiodiniaceae was significant, as previously reported by Santos et al. (2002), Baker (2003) and Takishita et al. (2003). This reinforces the idea of low divergence (Santos et al. 2002), and a parallel evolution of these two genes (Takishita et al. 2003). However, the results obtained from Symbiodiniaceae analyses differed according to the molecular marker used. It has been found that *Breviolum* sp. and *Cladocopium* sp. are closely related and difficult to differentiate based on rDNA markers (Wilcox 1998; Baker 2003). This could explain why some of the eastern Atlantic samples were related to *Cladocopium* sp., according to the ITS region, but not according to the 23S-rDNA. Similarly, Grajales and Sanchez (2016) also found difficulties in the identification of these two Symbiodiniaceae genera, even at the ITS2 resolution (see also LaJeunesse 2005). Multi-locus DNA analysis has been previously used to investigate the symbiont composition and variability within the host (e.g., Goulet and Coffroth 2003). The fact that the same coral samples showed different symbionts from different genera, according to the analysed genetic region, suggests than a heterogeneous pool of symbionts may exist within the same colony (see Fay and Weber 2012). Grajales and Sanchez (2016) found that *M. alcicornis* from the Caribbean hosted *Cladocopium* sp. and *Breviolum* sp. within the same colony. Similarly, our samples from the Canary and Cape Verde Islands showed *Cladocopium* sp. and *Breviolum* sp. in the same specimens. In addition, our specimens from Puerto Rico also showed a mixture of *Symbiodinium* sp. according to the 23S-rDNA marker, and *Breviolum* sp. according to the ITS-rDNA marker. In this sense, the results of RFLP of LSU-rDNA analysis suggest the possibility of several symbionts in the same host, at least in one sample from Tenerife.

Symbiont acquisition by a coral can occur via vertical transmission, where symbionts are transferred to the offspring, or via horizontal transmission, where symbionts are taken up from the environment through phagocytosis (Hirose et al. 2001; Weis et al. 2001; Stat et al. 2006, 2008). In the case of *M. alcicornis*, the medusae released during sexual reproduction harbour symbionts (vertical transmission) (Mangan 1909). However, our results indicated that the symbionts from the Canary Islands were more related to those from the Cape Verde

Islands than to those from the Caribbean, contrary to the hydrocoral results. This suggests that horizontal transmission may dominate, as a mechanism to acquire symbionts from the environment. The presence of different types of symbionts in the waters of the Canary and the Cape Verde Islands, and in some of their marine organisms, could be the potential sources for *M. alcicornis* uptake. For example, some zoanthids from the Canary Islands harbour the genus *Cladocopium* (C. López, personal communication), while *Symbiodinium natans* is present in the waters around the Canary Islands as a free-living dinoflagellate (Hansen and Daugbjerg 2009). Additionally, the genera *Symbiodinium*, *Brelovium*, and *Cladocopium* are also associated with some zoanthids from the Cape Verde Islands (Reimer et al. 2010a, 2017), and at least one stony coral (*Siderastrea radians*) also harbours the genus *Cladocopium* from the island of Sal (Monteiro et al. 2013).

An alternative explanation could be the existence of background symbionts of *Cladocopium* species that were not detected in the Caribbean samples, but that became more abundant, and therefore, detectable in the eastern Atlantic samples. This may occur because the abundance of the symbiont community within a single colony is not necessarily static. The colony can be flexible, changing their symbiont community by shifting existing background symbiont types, or by up-taking or expelling their symbionts depending on environmental conditions related to depth, light intensity or temperature (LaJeunesse 2002; Baker 2003; Iglesias-Prieto et al. 2004; Berkelmans and van Oppen 2006; Finney et al. 2010). According to Rowan and Knowlton (1995), *Symbiodinium* sp. and *Breviolum* sp. were normally associated with shallow depths in the Caribbean for *Orbibcella (= Montastraea)* spp., whereas *Cladocopium* sp. was found at greater depths. Our results showed no particular trend of *M. alcicornis* symbionts with depth, similar to Grajales and Sanchez (2016). However, the latitudinal gradient and the varying oceanographic conditions between the populations in our study should be considered when inferring the appearance of genera. *Cladocopium* sp. and *Breviolum* sp. have been associated with high latitude corals, which resist cold temperatures and extreme seasonal changes (Thornhill et al. 2008; Silverstein et al. 2011; Lien et al. 2012). These Symbiodiniaceae genera appeared in samples from the Canary Islands (28°N) and Cape Verde Islands (14 to 16ºN), located in areas influenced by the African upwelling and the cold Canary Current, where temperatures tend to be lower than expected for their latitudes, ranging from 18 to 25 °C (Clemente et al. 2010; Faye et al. 2015). After settlement in the Canary Islands, likely facilitated by temperature increases (Brito et al. 2005; Clemente et al. 2010; López et al. 2015), coral growth was probably possible due to the acquisition or "shuffling" of these cold tolerant symbiont types (detected as *Breviolum* sp. by the 23S-rDNA and *Cladocopium* sp. by the ITS region). *Symbiodinium* sp. seemed to show a preference for shallow and warm environments, since it appeared in Mexico and Puerto Rico samples, all located at depths < 7 m. The occurrence of *Symbiodinium* sp. in shallow waters coincides with LaJeunesse (2002) and Finney et al. (2010) and could be associated to its ability to protect itself from ultraviolet radiation (Banaszak et al. 2000; Reynolds et al. 2008). Although some of the samples from the Cape Verde Islands were also collected in the intertidal and shallow subtidal, no *Symbiodinium* sp. was found there. Despite the fact that the Cape Verde Archipelago was our southernmost eastern Atlantic study site, and that solar radiation is high at these latitudes, the mild temperature caused by the cold African upwelling and the Canary Current (Faye et al. 2015) may explain the absence of *Symbiodinium* sp. This fact also reinforces the idea of horizontal transmission or changes in background symbiont composition by *M. alcicornis* in the Cape Verde Islands.

There is some evidence that symbiont communities are changing due to climate change, so stress tolerance traits are selected by the holobiont (Baker et al. 2004; Parkinson and Baums 2014). These physiological traits vary between species of Symbiodiniaceae and also between strains (cultured isolates or subclades) within species (Díaz-Almeyda et al. 2017; Grégoire et al. 2017). For example, the dominant *Cladocopium* sp. was replaced by *Durusdinium* sp. in *Acropora millepora*, when seawater temperature increased in experimental conditions (Berkelmans and van Oppen 2006). *Durusdinium* sp. and some species of *Cladocopium* sp. (previously subclade C17) seem to be resistant to bleaching (Coffroth and Santos 2005), and *Symbiodinium* sp., *Durusdinium* sp. or *Effrenium* sp. usually appear in corals that have recovered from bleaching (Toller et al. 2001; Baker 2003; LaJeunesse et al. 2003). The aforementioned *Cladoscopium* sp. (C1) showed tolerance to low temperatures in corals from Japan (Lien et al. 2012) and from South Korea (De Palmas et al. 2015), explaining its presence at high latitudes. Similarly, some species (previously from subclade B2) of the genus *Breviolum* resisted temperatures of 10 °C under laboratory conditions (Thornhill et al. 2008); and the subclade B18 appeared in corals from temperate south-western Australia (33 °S) (Silverstein et al. 2011). Therefore, corals capable of changing their symbionts (through exogenous uptake or shuffling its internal symbiont abundance), depending on environmental conditions, can select the best genera to provide resilience to climate change (Baker et al. 2004; Berkelmans and van Oppen 2006). However, the ability of corals to exchange symbionts is reduced to a limited number of species (Iglesias-Prieto et al. 2004; Goulet 2006),

and only a few coral genotypes will be able to cope with extreme climatic changes (Goulet 2006).

Our results indicate that *M. alcicornis* has the capacity to up-take symbionts from the environment ("horizontal transmission"), or to change the abundance of its internal symbionts types. Either of these mechanisms allows the species to acclimatize to the surrounding environmental conditions. Poleward coral expansions have been reported in the last decades due to climate change (Vargas-Ángel et al. 2003; Greenstein and Pandolfi 2008; Yamano et al. 2011). If sea water temperature keeps increasing according to the IPCC scenarios, the expansion of *M. alcicornis* to other subtropical or temperate regions could also occur. Therefore, the presence of this species in new regions, and the flexibility of the coral to adapt to the new conditions, would depend on the pool of available symbionts, whether inside the host or in the surrounding seawater. The collection and further DNA analyses of samples, taken at different seasons and over several years, would help to elucidate if the hydrocoral has a rapid ability to change their symbionts under different conditions (Stat et al. 2006). Additionally, further research on the transcriptome of *M. alcicornis* (see Ortiz-González et al. 2017), as well as the extraction of information about its symbionts, would improve the scientific knowledge about the holobiont response to environmental changes.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Chapter 6: General Discussion

This thesis investigates the potential distributional shifts of tropical corals under climate change by projecting the current and predicting the future habitat suitability of these species. In order to make reliable predictions, the environmental factors driving corals distributions were studied based on modelling techniques of Species Distribution Models (SDMs). The environmental variables (climatic and physiochemical) that most affected corals' distributions were: sea surface temperature, salinity, phosphate, photosynthetic active radiation, pH, diffuse attenuation of the water column and cloud cover. Their relevance varied depending on the scale and region of study; except temperature which is usually the most important at all scales. Temperature varies according to the latitude (lower temperatures at higher latitudes), but also according to the ocean currents, with a general pattern of warmer temperatures at the western ocean basins and colder temperatures on the eastern basins due to the Coriolis effect. Temperature is normally the most important variable driving corals distribution because it controls many physiological processes as respiration and calcification that directly affect the normal function of reef building corals (Jokiel and Coles 1977; Naumann et al. 2014), or the symbiotic relationship with corals' symbionts (Cumbo, van Oppen, & Baird, 2018). Temperature presents a large variation also at regional or local scales, with microclimates enhancing/diminishing corals development. If the temperatures increase because of climate change, corals that currently live close to their upper thermal thresholds may die if those rising temperatures are higher than their thermal limits, and no adaptation occur within the new conditions. Acidification decreases coral calcification and coral growth through the inhibition of aragonite formation (Hoegh-Guldberg et al., 2007; Kleypas & Langdon, 2006). Acidification is causing isolines of aragonite concentration moving southward, potentially limiting temperature induced poleward expansions of coral habitats (Yara et al., 2012), at very high latitudes (e.g. in Japan). Ocean salinity mainly varies at river mouths; thus, its impact is more local than global. The lack of phosphate and other inorganic nutrients are typical of eutrophic tropical regions where coral reefs flourish thanks to their associated symbionts. High levels of inorganic nutrients mostly occur at high latitudes, but they are also related to local waste discharges and runoff due to deforestation (McCulloch et al., 2003), which can have adverse effects on corals. Such effects are lowering corals calcification (Chefaoui et al., 2017; Dunn, Sammarco, & LaFleur, 2012); magnifying their susceptibility to diseases; or increasing their competition with macroalgae, increasing the proliferation of filamentous algae which can

overgrowth corals and cause their death (Jompa & McCook, 2003). Low photosynthetic active radiation (PAR) levels usually restrict corals distribution to low latitudes; but in some local areas the high diffuse attenuation of the water column also does not allow the sunlight to penetrate the water column, making light insufficient for photosynthesis (Castro & Huber, 1997; Lesser et al., 2009; Nybakken & Bertness, 2001). Continental coasts generally have more land erosion and pollution than archipelagos, what is associated with turbid waters, via terrestrial runoff (Fabricius, 2005). Cloud cover also varies locally, especially in the Intertropical Convergence Zone (ITCZ), a tropical storm band produced by the convergence of the warm and humid trade winds of the northern and southern hemispheres. Unravelling how these variables affect the distribution of corals broadens our understanding to promote mitigation actions. Many coral reef conservation strategies are only focused on a local scheme, studying exclusively local threats such as coastal development, and destructive fishing techniques (Souter & Linden, 2000). But most of these areas are also at high risk of severe climate-related degradation, as ocean temperature increases or acidification, as aforementioned. Hence, the combination of local approaches with global or regional scale research can reduce conservation failures (Harris et al. 2017; Beyer et al. 2018). Importantly, some climatic variables can be correlated with other parameters not accounted in the models. For example, distance to the coast can be correlated to temperature, and it might be the principal factor influencing the distribution of a species in a local scale instead of temperature. Expert knowledge can help to elucidate these issues. Thus, a comprehensive ecological study of the main factors affecting species distributions must guide the steps of the variable selection in the modelling process, not only the statistical results.

The study of coral distributional shifts generates new knowledge based on the potential range contractions and expansions of corals, which is advisable for their conservation. In particular, we demonstrate in this thesis (Chapter 2) that the Indo-Pacific coral *P. varians* will completely decrease their habitat suitable by the year 2100 even under an 'intermediate' climate change scenario (A1B) despite being considered an opportunistic species. Also, the Atlantic corals *Agaricia fragilis*, *Manicina areolata*, *Oculina varicosa*, *Porites colonensis*, *Scolymia cubensis*, *Siderastrea radians* and *Solenastrea hyades* will practically decrease all their potential current habitat suitable under the most severe scenario (A2) by the year 2100. Most of the Atlantic scleractinian corals of our study (32 species) (Chapter 3) and the hidrocoral *M. Alcicornis* (Chapter 4) will also decrease their potential habitat suitable by the year 2100, specially in

some tropical areas, such as the Caribbean Sea; but in the meantime, they will also increase their habitat range to higher latitude; (if their dispersion capacities and competition abilities will allow them to migrate and settle into those new areas). Only five species, *Agaricia teunifolia*, *Diploria clivosa*, *Madracis pharensis*, *Mycetophyllia larackiana* and *Porites furcata* are predicted to expand their potential range in the Atlantic without suffering any range contraction in their current habitat suitable. And only *Solenastrea bournoni* will not experience any change its current habitat suitability index. The information extracted for each species can be used in conservation plans to conserve coral reefs. However, despite these informative results, it is important to mention that projecting regional species habitat suitability under current and future different IPCC climate scenarios (with future conditions non-analogous to the current ones) is a challenge, and some limitations may arise. As mentioned above, sea surface temperature is one of the main factors that most affect the physiology of corals and, therefore their survival and distribution (Chapters 2, 3, 4 and 5). Moreover, it is the environmental factor with the most information available on future projections and, therefore widely used for making predictions. Increases of temperature are causing diseases and bleaching on corals, and ultimately can cause coral's death. These increases can produce species extinctions in those areas where the temperature exceeds the thermal limits of the corals. However, these extinctions are not always detected by SDM predictions because most corals live close to their upper thermal limits, and their thermal response curves (based on current environmental range conditions) are truncated, because no decline is detected at current temperatures (Anderson, 2013). However, future conditions can be lethal for some of species (if their thermal threshold is exceeded), and this is might not be captured by the classical SDM projections. In those cases, the novel contribution proposed in this thesis (Chapter 3) overcomes this constrain by incorporating the thermal physiological information of the species into the denominated Hybrid SDM. The inclusion in the model of the complete physiological thermal response of the species, by carrying out manipulative experiments, makes it possible to have the complete response of the organism to all thermal conditions (both present and future). This information is then incorporated into the SDM as a new input variable, by applying the response curve to a temperature raster to create a new physio-climatic variable, which was then integrated into the Hybrid SDM as a predictor. This new method allows predictions without extrapolations in the physio-climatic predictor, predicting a decline in the habitat suitability of the species studied (*M. alcicornis*), unnoticed by the correlative model; and also incorporated

the habitat suitability restrictions of other predictors of unknown physiological response. The method proposed could also be applied to other environmental variables affecting the physiology of the species, which also need extrapolation to future conditions. However, species-specific physiological information is not commonly available, and experiments are arduous and time consuming. Therefore, an increment on species physiological research should also be promoted for improving Hybrid SDMs. A limitation of this approach is that it does not consider the coral's capacity to adapt over time. Thus, acclimation or adaptation experiments could reinforce this issue improving predictions (Logan et al. 2014; Parkinson and Baums 2014).

Coral distributional shifts (Chapters 2, 3, 4 and 5) can trigger other changes in some ecological aspects of the reef systems; such as changes in the richness or phylogenetic diversity of the coral assemblages (Chapter 3). The combination of distributional shifts and phylogenetic analyses carried out in this thesis did not only inform about the occurrence or disappearance of certain coral species in some regions (mentioned above); but it also reveals potential changes in the structure of Atlantic reef communities. Therefore, one of the aims of chapter 3 was to test whether the predicted distributional changes of Atlantic corals would be randomly distributed or clustered across the coral's phylogeny. These predictions obtained must be accounted when developing operative plans to set prioritization areas of conservation, because they do not only account for potential species richness decrease, but also for potential losses of highly relevant species from a phylogenetic perspective (evolutionary history) (Erwin, 1991; Tucker et al., 2017). According to our results, the potential future loss of Atlantic corals will be randomly distributed across the phylogeny. Thus, future extinctions will occur independently on their lineages. Despite the negative consequence of losing species, the random distribution of these changes means that contractions will not only affect to one section of the phylogeny, which could cause an inordinate loss of evolutionary history. In other words, expected retractions of Atlantic corals will affect indistinctly to all lineages. Therefore, potential effects on the phylogenetic diversity of the coral community will vary depending on the species disappeared/appeared in each site. Species belonging to isolated clades (high evolutionary distinctiveness) will contribute to quantitative increases or decreases of Phylogenetic Diversity (PD) and Phylogenetic Species Variability (PSV); becoming crucial species for conservation. The combination of SDMs with phylogenetic analyses also informs about which areas could have large evolutionary diversity losses, and hence are of potential

conservation interest. These areas are mostly tropical areas (as the Caribbean) with high bleaching probabilities due to high temperatures (Winter et al. 1998; Eakin et al. 2010). Conservation, and lastly, restoration actions should be active in these regions. On the contrary, other areas (usually current warm-temperate regions) will increase their PD, becoming potential refuges, if the species are able to migrate and settle there. These are therefore areas of special interest, particularly if the areas of origin are not successfully preserved. However, most of these areas already have their native fauna and flora, and thus, the arrival of tropical corals may cause ecological problems by out-competing, for example, with native macroalgae (Serrano et al. 2013; Vergés et al. 2014; Wernberg et al. 2016). Our approach does not account for competition interactions or species dispersions, which would improve the robustness of the results. Another limitation results from the construction of the model with only presence data. In some regions, this may cause omission errors, i.e. classifying areas as presence, where the species is not present. However, this cannot always be accounted, because many regions, as for example the Western coast of Africa, have not been thoroughly explored and their sampling efforts are low. Model evaluation provides confidence in predictions, but as shown in Chapter 4, when extrapolations fall outside the training range of the data, these indices are not always correct, and the consideration of other uncertainty parameters, such as the 'Most dissimilar variable' (MoD) (Elith et al. 2010) can be very useful (Owens et al. 2013). Despite all the limitations of SDMs due to the inherent complexity of natural systems, their combination with physiological information, genetic and phylogenetic analyses, provides the convenient framework to assess the potential effects of climate change on biogeographic patterns.

On chapters 2 and 3, features 'linear', 'quadratic' and 'hinge' were used in MaxEnt, because no species-specific physiological information was available, and thus the Hybrid model could not be applied. In these cases, the 'hinge' setting is normally adequate to detect environmental thresholds, although, simpler features such as 'linear' or 'quadratic' are more recommended for making projections (Austin 2002; Elith et al. 2010; Moreno-Amat et al. 2015). Even with the 'hinge' feature, some thresholds might not be detected, as they may only occur at high temperatures which only exist in future projections. In these cases, predictions should be taken with caution. MaxEnt currently only permits to set the same setting for all the environmental variables selected. Thus, an improvement for its better performance would be the possibility of choosing different settings depending on each environmental variable; i.e. being able to set, for example, the *temperature* with 'hinge' and *salinity* with 'linear'. Even better, it would be ideal

the possibility to manually include lethal values. Following this strategy, any user could guide the extrapolation based on the scientific literature. Other methods, such as generalized additive model (GAM) with weighted distribution of pseudoabsences (Zaniewski et al. 2002), which allows the researcher to choose among 'linear', 'quadratic', 'cubic' and so on, for each variable, might be an option. However, they can neither include future lethal trends, and its performance with only presence data should be compared to that of MaxEnt. Despite SDMs have some limitations, such as not accounting for interspecific interactions or species dispersion capacities (Sinclair et al. 2010), they still provide a relevant scientific basis for guiding conservation decisions. Detecting these limitations (Owens et al. 2013) and developing new methods, such as the Hybrid SDM, to solve them, contribute to improve the applicability of SDMs in conservation decision making (Guisan et al. 2013).

As mentioned above, SDMs do not only detect areas of potential extinctions, but also potential areas of expansion; as observed by the habitat suitability projections of most of the corals studied in this thesis (~80%). Distributional expansions of species are generated as a way of escape from stressful factors (mainly climatic, but also biotic), pursuing new oases where they can survive. Therefore, temperature increases also creates new habitats (or refuges) for tropical corals at higher latitudes (Beger et al. 2014); (as long as other factors, such as ocean acidification (Yara et al., 2012) or nutrients are kept at constant current levels allowing corals to survive there and compete with the local species). To reach these refuges, species must be able to disperse long distances (e.g. thousands of kilometres) and overcome biogeographical frontiers (e.g. major river mouths such as the Amazon). Major boundary current systems usually facilitate coral larval transport from tropical to subtropical waters (Booth et al., 2007). However, when this information is unknown, or there are no evidences to support a determined dispersal pathway, genetic analyses can help to elucidate potential dispersal patterns. In chapter 5, the genetic origin of the new population of *M. alcicornis*, appeared in the Canary Islands, along with their symbionts ware identified. Due to its proximity to the Cape Verde Islands, one plausible hypothesis was the origin of the hydrocoral from those islands. However, our research confirmed the results obtained by López et al. (2015), establishing the genetic origin of *M. alcicornis* as the Caribbean region, from where it could have been rafted by the Gulf Stream. Conversely, in our study, *M. alcicornis*' symbionts were more closely related to the symbionts from Cape Verde Islands (East Atlantic) than to those from the West Atlantic. This genetic mismatch between coral host and symbionts suggests that *M. alcicornis* has the capacity to up-

take symbionts from the environment ("horizontal transmission"), or to change the abundance of its internal symbiont types. Either of these mechanisms allows the species to acclimatize to the surrounding environmental conditions. Some experiments tested that high latitude populations of marine organisms can outperform their low-latitude counterparts when temperatures are above the local average (Conover et al. 2009; Gardiner et al. 2010; Beger et al. 2014). This could be attributed to a greater phenotypic plasticity in populations living at higher latitudes, because they are acclimated or adapted to a greater thermal variability than tropical populations, also indicating that they could be more resistant to altered environmental conditions (Beger et al. 2014). Such an outcome is essential for corals to survive under the scenarios of global warming (Baums, 2008). Thanks to the genetic analyses of the hydrocoral, *M. alcicornis*, and their symbionts, we elucidated the relationships between its geographically isolated populations, and thus established its potential patterns of origin and dispersion, as well as identify its ecological mechanisms of adaptation to the environment.

In summary, corals health is declining because of climate change effects (Hughes et al. 2003, 2010); and the predictions based on the suitability of their habitats indicate that ~87% of the corals studied in this thesis may become extinct in certain regions, if active conservation measures are not urgently implemented. Coral reefs are one of the most diverse and productive marine ecosystems in the world providing vital ecosystem services to human societies and industries (Moberg and Folke 1999; Hoegh-Guldberg et al. 2007) and its conservation must be a priority. However, there is still a limited knowledge about coral reef ecosystems (Beger et al. 2011). A global dense sampling of corals, inventory of DNA sequences (Knowlton et al. 2010) and intensive species physiological studies, would provide reliable information for estimating corals biodiversity across space and time which is essential for protecting these ecosystems. In conclusion, there exist a critical need to combine the scientific research outputs with the decision-making processes for improving the conservation of the reef communities (Beger et al. 2014), and this thesis aimed to provide that integrative framework by exploring different methodological approaches to better understand the future fate of tropical corals. Global management strategies supporting reef resilience and adaptation, need to be implemented, along with solid policy decisions to reduce the rate of global warming (Hughes et al. 2003).

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Chapter 7: General Conclusions

This thesis has generated an integrative knowledge of the most relevant ecological responses of tropical corals undergoing climate change.

1. The most important variables driving corals distribution may differ according to the species and scale of the study, varying among sea surface temperature, salinity, diffuse attenuation of the water column, cloud cover, photosynthetic active radiation, pH and phosphate.

2. It is expected that *Millepora alcicornis*, as well as most of the tropical corals (~87%) studied in this thesis, will suffer range retractions at low latitudes where future temperatures will feasibly exceed their thermal tolerances.

3. It is predicted that *Millepora alcicornis*, as well as other Atlantic tropical corals (~80%), will expand their range to higher latitudes due to poleward shifts of tropical currents that transfer warm conditions to subtropical and temperate latitudes.

4. Integrating physiological knowledge into Hybrid SDMs by adding a physio-climatic predictor improves model transferability, resulting in predictions of decline in future climates, which may be misrepresented by classic SDMs.

5. SDMs can be used for detecting potential areas of corals extinction or invasion, assessing the potential effects of climate change on biodiversity and guiding conservation actions.

6. The potential future loss of Atlantic corals will be randomly distributed across the phylogeny, alleviating an inordinate loss of evolutionary history. Nearly all current and future communities present random phylogenetic structures.

7. Predicted changes in Atlantic coral Richness, PD, and PSV vary across the Atlantic. Certain areas under predicted large evolutionary diversity losses are of potential

conservation interest. Species belonging to isolated clades (high evolutionary distinctiveness) contribute to quantitative increases or decreases of PD and PSV, becoming crucial species for conservation actions.

8. There exist a high genetic variation of *M. alcicornis* within and between both sides of the Atlantic, establishing the Caribbean (West Atlantic) as the origin of the recently established colonies in the Canary Islands; on the other hand, their associated symbionts are more related to those from the Cape Verde Islands (East Atlantic).

9. The genetic mismatch between *M. alcicornis'* coral host and its symbionts suggests that *M. alcicornis* may have an "horizontal" symbiont acquisition from the environment, or the ability to change its internal symbiont composition according to the conditions of the environment.

10. The combination of different ecological approaches as SDMs, phylogenetic and genetic analyses optimizes and generates early warning tools for conservation management.

Supplementary materials

- Supplementary materials Chapter 2: Environmental factors driving the distribution of the tropical coral *Pavona varians*: predictions under a climate change scenario

Table S1 Environmental variables extracted from Bio-Oracle (resolution of 0.08º, ~9.2 km); Table adapted from Tybergheim *et al*. 2012.

Acronym	Variable	Units	Origin
Chlomax [a]	Max chlorophyll *a* concentration	mg m^{-2}	Temporal maximum from monthly climatologies (2002–2009)
Chlomin [a]	Min chlorophyll *a* concentration	mg m^{-2}	Temporal minimum from monthly climatologies (2002–2009)
Cloudmax [b]	Max cloud cover	%	Temporal maximum from monthly images (2005–2010)
Damax [a]	Max diffuse attenuation (turbidity of the water column)	m^{-1}	Temporal maximum from monthly climatologies (2002–2009)
DissOx [c]	Dissolved oxygen	ml l^{-1}	DIVA interpolation of in-situ measurements
Nitrate [c]	Nitrate	µmol l^{-1}	DIVA interpolation of in-situ measurements
Parmax [d]	Max photosynthetically available radiation	Einstein m^{-2} day^{-1}	Temporal maximum from monthly climatologies (1997–2009)
pH [c]	pH	-	DIVA interpolation of in-situ measurements
Phosphate [c]	Phosphate	µmol l^{-1}	DIVA interpolation of in-situ measurements
Salinity [c]	Salinity	PSS	DIVA interpolation of in-situ measurements
SSTmax [a]	Max sea surface temperature	°C	Temporal maximum from monthly climatologies (2002–2009)
SSTmin [a]	Min sea surface temperature	°C	Temporal minimum from monthly climatologies (2002–2009)

Type of source: [a] Bio-ORACLE - Aqua-MODIS, [b] Bio-ORACLE - Terra-MODIS, [c] Bio-ORACLE - WOD 2009, [d] Bio-ORACLE – SeaWiFS.

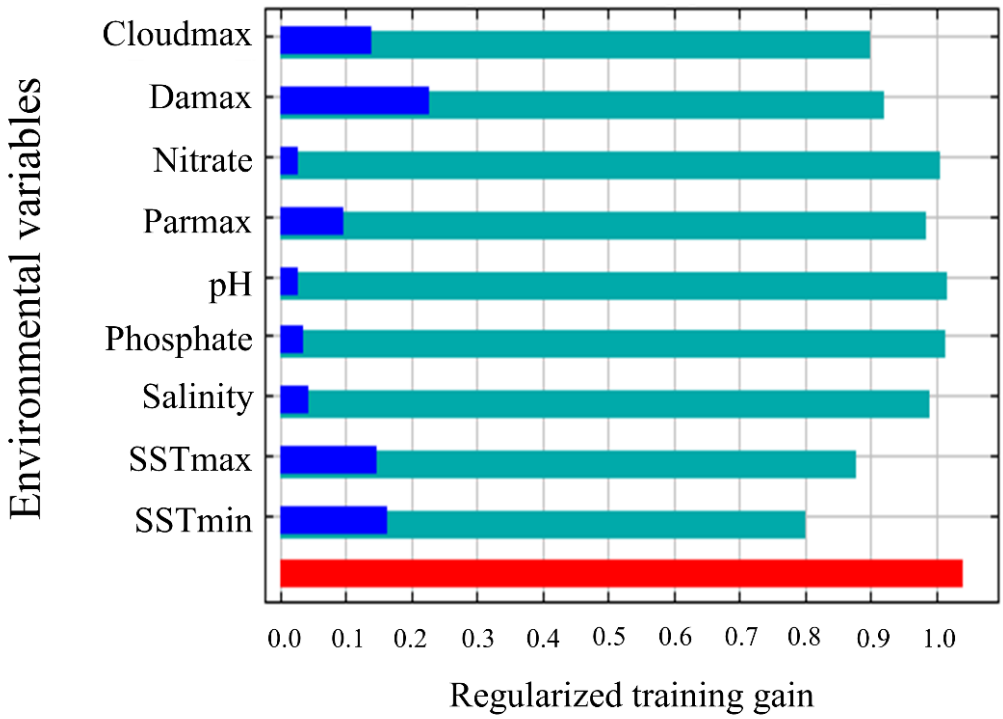


Fig. S1 Jackknife test. The red bar indicates the total gain of the model with all variables. Dark blue bars indicate the information given to the model by each variable. Light blue bars represent the gain of the model when one of the variables is omitted. If the gain is highly reduced when one variable is omitted, then that variable is important for the model.

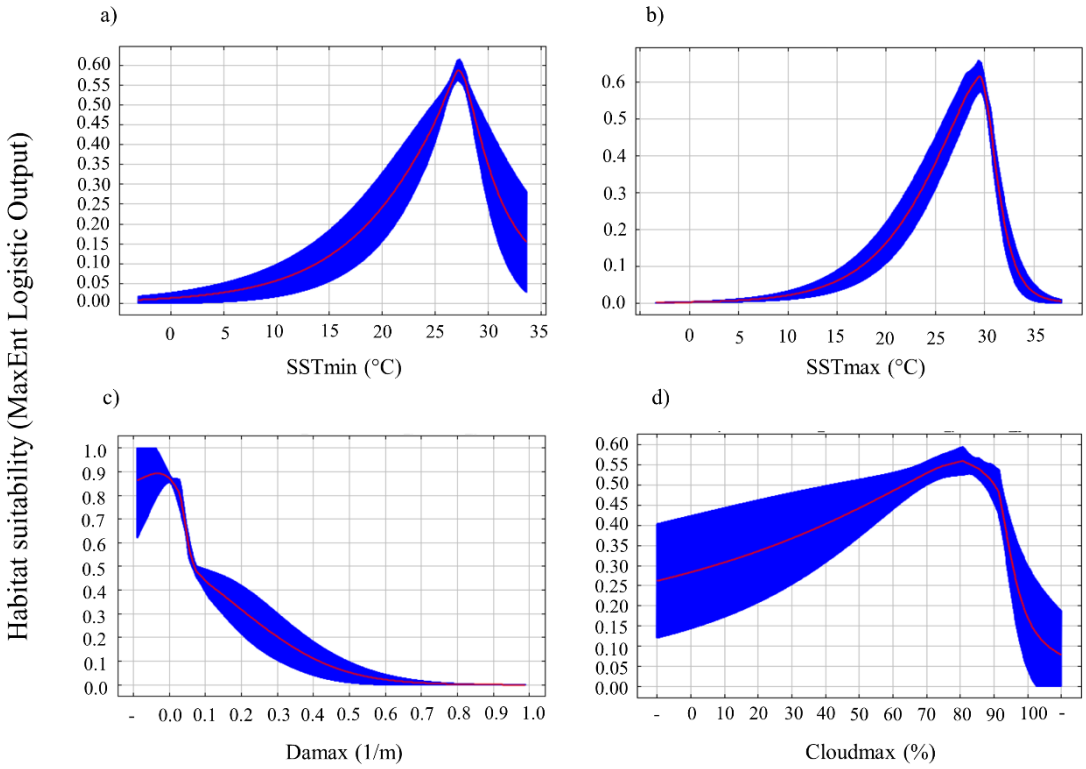


Fig. S2 *Pavona varians* response curves obtained by MaxEnt for SSTmin, SSTmax, Damax and Cloudmax. The red line represents the mean logistic habitat suitability, and the blue area the ±1 standard deviation based on 10 replicate runs.

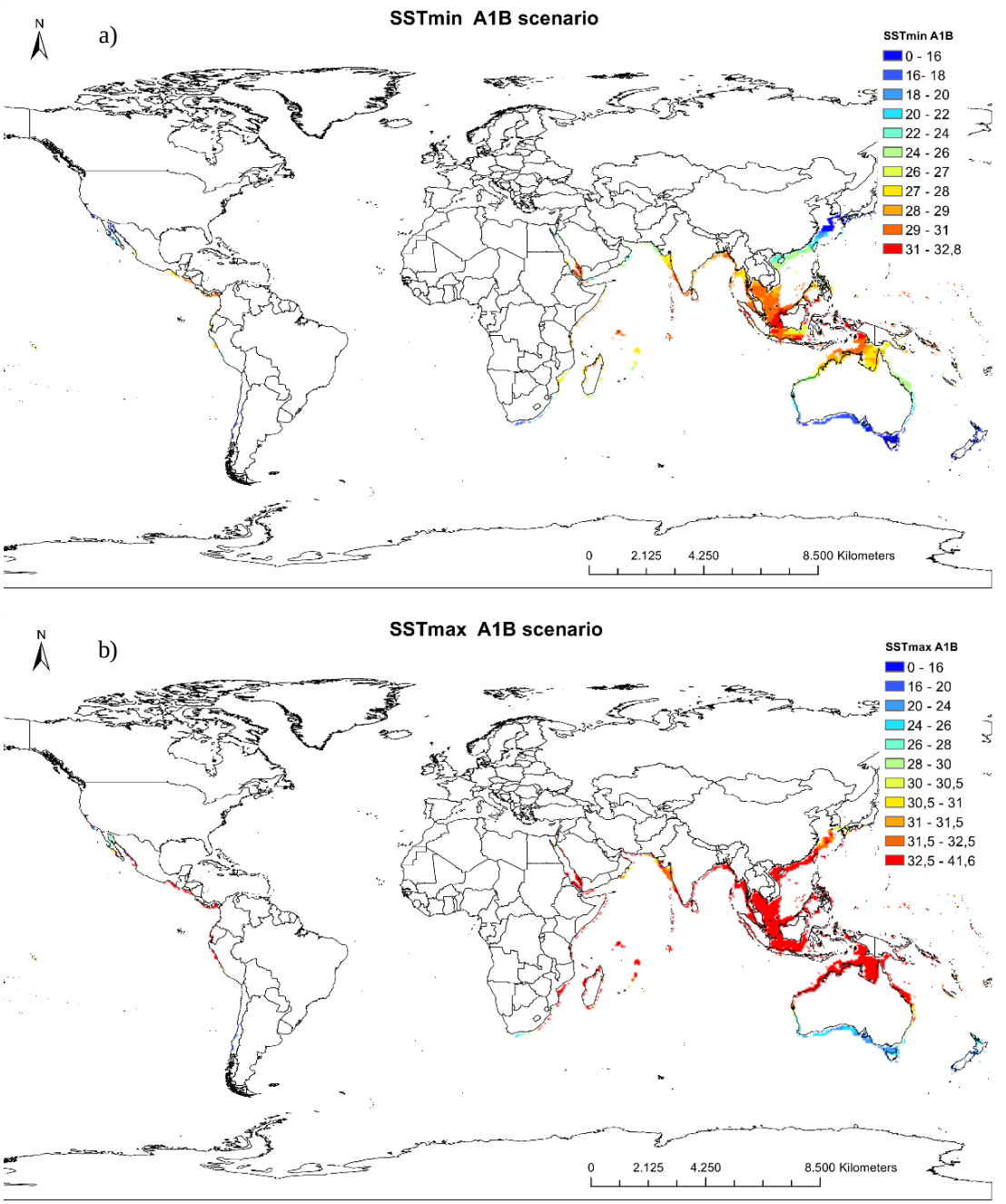


Fig. S3 Gradient maps of (a) SSTmin and (b) SSTmax under a A1B scenario for the year 2100.

- Supplementary materials Chapter 3: Atlantic corals under climate change: modelling distribution shifts to predict richness, phylogenetic structure and diversity changes

Table S1. Environmental variables extracted from Bio-Oracle (resolution of 0.25º); table adapted from Tybergheim *et al.* (2012). Variables finally selected by each SDM are highlighted in bold.

Acronym	Variable	Units	Origin
Chlomax [a]	Max chlorophyll *a* concentration	mg m^{-2}	Temporal maximum from monthly climatologies (2002–2009)
Chlomin [a]	Min chlorophyll *a* concentration	mg m^{-2}	Temporal minimum from monthly climatologies (2002–2009)
Chlomean [a]	Mean chlorophyll *a* concentration	mg m^{-2}	Temporal minimum from monthly climatologies (2002–2009)
Cloudmax [b]	Max cloud cover	%	Temporal maximum from monthly images (2005–2010)
Damax [a]	Max diffuse attenuation (turbidity of the water column)	m^{-1}	Temporal maximum from monthly climatologies (2002–2009)
DissOx [c]	Dissolved oxygen	ml l^{-1}	DIVA interpolation of in-situ measurements
Nitrate [c]	Nitrate	µmol l^{-1}	DIVA interpolation of in-situ measurements
Parmax [d]	Max photosynthetically available radiation	Einstein m^{-2} day^{-1}	Temporal maximum from monthly climatologies (1997–2009)
pH [c]	pH	-	DIVA interpolation of in-situ measurements
Phosphate [c]	Phosphate	µmol l^{-1}	DIVA interpolation of in-situ measurements
Salinity [c]	Salinity	PSS	DIVA interpolation of in-situ measurements
SSTmax [a]	Max sea surface temperature	°C	Temporal maximum from monthly climatologies (2002–2009)
SSTmin [a]	Min sea surface temperature	°C	Temporal minimum from monthly climatologies (2002–2009)
SSTmean [a]	Mean sea surface temperature	°C	Temporal minimum from monthly climatologies (2002–2009)
Aragonite	Aragonite	Ω	Couce, 2012: Output from the program CO2sys using alkalinity and total CO2 from GLODAP (Key et al., 2004), SST, salinity, silicate and phosphate data from WOA 2005. Missing regions filled with output from the UVic Earth System Climate Model (Weaver et al., 2001; Turley et al., 2010) following the method outlined in Cao & Caldeira (2008).
Light			

Type of source: [a] Bio-ORACLE - Aqua-MODIS, [b] Bio-ORACLE - Terra-MODIS, [c] Bio-ORACLE - WOD 2009, [d] Bio-ORACLE – SeaWiFS.

Table S2. Summary of the percent contribution coefficients explained by each environmental variable, as provided by MaxEnt. Percent contribution (Contr.) and Permutation importance (Imp.). The variables with the highest percent contribution and highest permutation importance are highlighted in bold, for each species (Values > = 20%) are denoted with an asterisk (*). Area under the curve (AUC) representing the accuracy of the model.

Species	**Sstmean**		**Phosphate**		**Salinity**		**pH**		**Damax**		**Parmax**		**AUC**
	Contr	Imp	Contr	Imp	Contr	Imp	Contr	Imp	Contr	Imp	Contr	Imp	
Acropora cervicornis	38.4*	**64.1***	**40.8***	3.3	11.5	18.3	2.2	6.4	5.6	3.5	1.4	4.3	0.940
Acropora palmata	37.1*	**59.1***	**43***	6.1	9.1	19.5	4.4	10.6	4.4	0.6	1.9	4.1	0.930
Agaricia Agaricites	**42***	**65.9***	30.5*	0.4	10.4	19.1	6.2	9.9	9.4	2.2	1.6	2.6	0.939
Agaricia fragilis	22.9*	12.5	**51.3***	**58***	4.8	13.8	8	4.9	11.1	0.5	2	10.2	0.923
Agaricia grahamae	23.3*	**39***	**44.5***	5	1.3	8.2	0.8	19.1	27.3*	18	2.7	10.7	0.948
Agaricia humlilis	6.1	9.2	19	18.1	**65.7***	**46.4***	2.5	18.9	5.7	1.7	1	5.7	0.957
Agaricia lamarcki	23.8*	**47.6***	**59.4***	15.6	9.7	24.5*	4.1	9.5	0.9	0	2.1	2.9	0.941
Agaricia teunifolia	29.3*	**38.6***	**44.4***	9.5	4.2	33.6*	10.5	9.8	5.3	1.7	6.3	6.8	0.967

Agaricia undata	31.3*	18.7	**43.1***	**27.5***	9.8	25.7*	8.7	21.2 *	4.6	0.2	2.6	6.7	0.963
Colpophyllia natans	**40.8***	**55.6***	36.5*	1	7.5	20.3*	6.7	15.6	5.7	1.6	2.7	5.8	0.923
Dendrogyra cylindrus	35.2*	**61.8***	**46.4***	3.1	4.2	17.9	6.4	12.8	7.5	2.6	0.3	1.7	0.947
Diploria clivosa	23.6*	**46.3***	**56.4***	11.6	6.5	18	5.1	11.3	2.7	2.8	5.7	10	0.946
Diploria labyrinthiformis	27	**64.9***	**48.1***	4.9	5.9	14.6	4.5	9.6	11.8	2.2	2.6	3.8	0.942
Diploria strigosa	37.5*	**65.5***	**45***	3	9.8	17.2	4.8	11.3	2.3	0.6	0.7	2.3	0.938
Eusmilia fastigiata	38.3*	**51.3***	**38.4***	0.4	7	25	3.9	10.1	8.6	6	3.9	7.2	0.941
Favia fragum	19.1	**58.9***	**68.3***	13.8	2.4	16.4	1.5	0.3	2.5	0.9	6.2	9.8	0.928
Helioseris cucullata	**42.6***	**66***	26.7*	17.7	7.4	4.3	3.2	6.2	19.7	4.6	0.4	1.3	0.903
Isophyllia sinuosa	12.2	0	**80.2***	**84***	1.4	1.1	2.8	7.1	2.9	2.5	0.5	5.2	0.961

Madracis decactis	**49.3***	**55.5***	19.2	1.1	4.7	14.5	7.4	17.2	17.2	3.7	2.2	8	0.903
Madracis formosa	**53.6***	**49.7***	12.9	1.3	5.8	8.6	9.9	31	17.8	9.4	0	0	0.931
Madracis pharensis	12	**57.9***	**60***	21.7*	0.8	0.6	1.7	8.1	23.6	10.5	1.9	1.1	0.883
Manicina areolata	4.1	3.2	**85.8***	**67.5***	4.4	18.5	3.4	4.8	0.8	2.4	1.6	3.6	0.899
Meandrina meandrites	36.2*	**56.3***	**44.7***	1.3	5.8	21.6*	8.4	14.5	2.1	0.9	2.8	5.5	0.931
Montastraea annularis	35*	**61.5***	**37.1***	2.3	8.4	15.9	6.7	12.4	9.6	2.6	3.1	5.3	0.942
Montastraea cavernosa	35.4*	**44.5***	**36.5***	2.5	10.5	25.9*	6.2	14.6	8.6	5.6	2.9	6.8	0.913
Montastraea faveolata	37.2*	**60.6***	**39***	2.3	13.2	22.4*	5.3	10.3	4	0.4	1.3	4.1	0.938
Montastraea franksi	**46***	**60.4***	29.1*	0.2	6.7	20.1*	12.3	13.4	4	1.8	1.9	4.2	0.949
Mussa angulosa	37.8*	**42.9***	9.1	2.1	**41.3***	29.4*	6	18.9	5.1	2.2	0.7	4.5	0.902

Mussismilia harttii	8	0	12.4	41.5*	**76***	**42.7***	0.7	8.4	3	7.4	0	0	0.934
Mussismilia hispida	2.2	0	12.9	9.2	**82.1***	**90***	0.7	0.8	2	0	0	0	0.953
Mycetophyllia aliciae	19	27*	**49.2***	**33.2***	10.4	20.7*	7	4.6	14.5	14.5	0	0	0.958
Mycetophyllia danaana	**42.7***	**32.2***	40.7*	30.2*	12.2	36.3*	4.1	1.3	0.2	0	0	0	0.986
Mycetophyllia lamarckiana	31.2*	34.8*	**52.5***	**36.7***	3.7	18.8	2.3	4.1	5.3	2.1	5	3.5	0.950
Oculina varicosa	7.5	2.6	**65.2***	**42.3***	8.4	21.7*	13.9	31.2*	4.5	0.1	0.5	2.1	0.968
Porites astreoides	34.9*	**46.7***	**44.1***	5.6	9.2	24*	5.6	13.1	2.8	1.8	3.5	8.8	0.923
Porites branneri	17.1	8.9	2	0	**69.6***	**73***	0.4	1.9	9.8	5.9	1.2	10.3	0.926
Porites colonensis	3.6	0.7	**72.9***	**84.5***	3.7	0.5	1.5	0.3	4.7	5.6	13.5	8.5	0.989
Porites furcata	40.1*	36.2*	**46.4***	**38.2***	6.7	1	3.3	5.6	3.2	0.1	0.3	1.9	0.954
Porites porites	**40***	**61.8***	35.5*	1.8	12.6	19.7	4.1	11.3	6.1	1.4	1.6	4	0.932

Scolymia cubensis	29.2*	11.7	**39.4***	**27.6***	21.3*	27.4*	1.5	5.1	3	2.3	5.5	25.8*	0.930
Siderastrea radians	22.3*	4.9	**60.6***	**39.3***	5.1	37.5*	7.7	8.5	3	2.9	1.3	6.9	0.902
Siderastrea siderea	32.8*	**42.2***	**52.9***	4.1	8.3	31	3.2	13.4	0.5	1.6	2.3	7.7	0.913
Solenastrea bournoni	19.9	20.4*	**62.8***	**33.6***	4.4	29.3*	5.7	9.7	4.3	3.2	3	3.9	0.955
Solenastrea hyades	21.9*	11.8	**56.7***	**83.1***	7.1	2.8	1.8	0.5	12.4	1.8	0.1	0.1	0.989
Stephanocoenia intersepta	33.2*	**60.3***	**45.6***	0.1	9.1	20.3*	5.4	15.7	5.9	1.6	0.8	1.9	0.914

Excellent AUC>0.90; good 0.90-0.80; fair 0.8-0.7; poor 0.7-0.6; fail 0.6-0.5 following (M. Araújo et al., 2005) adapted from (Swets, 1988).

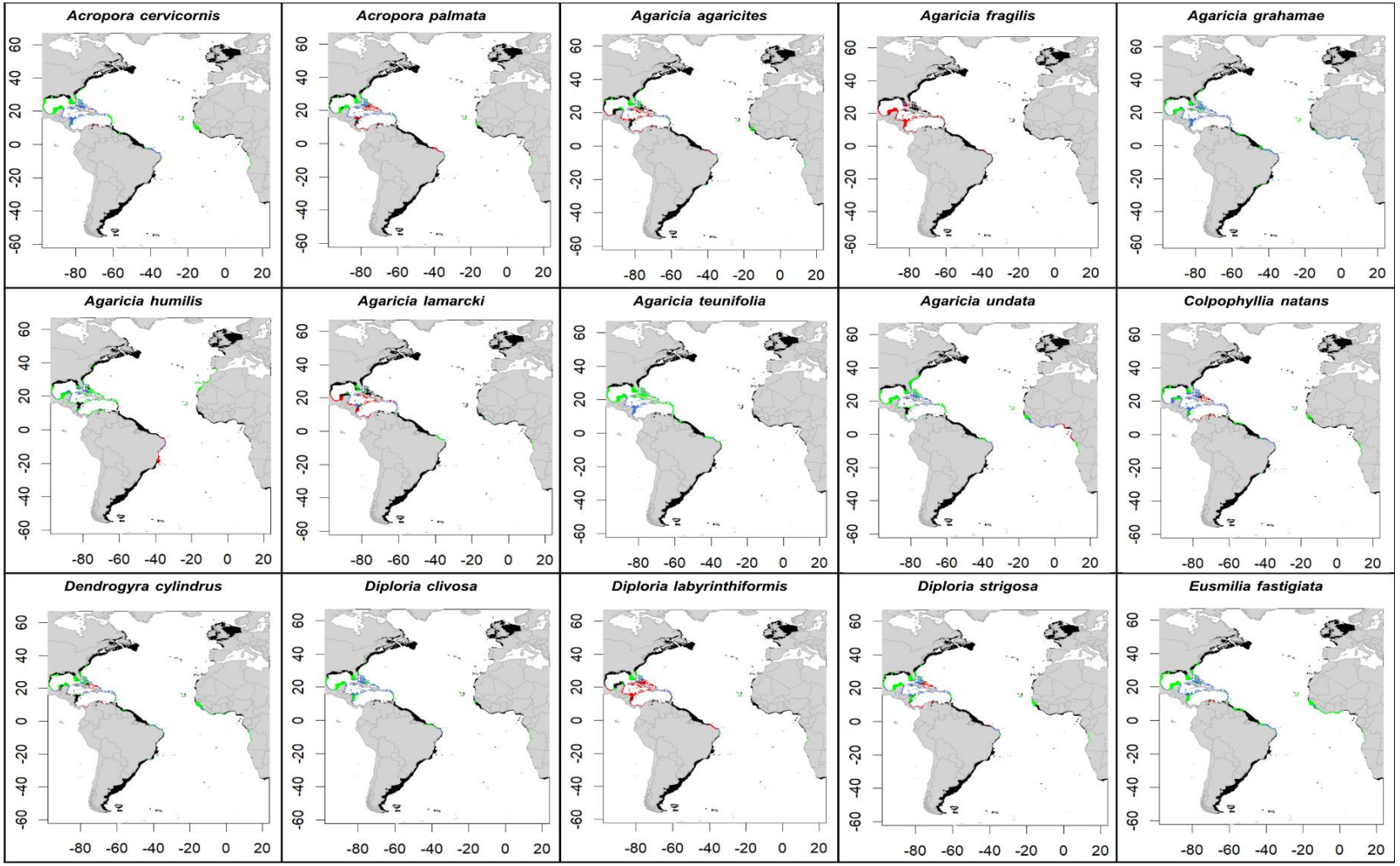
Table S3. Spearman correlations of the environmental variables and the phylogenetic dissimilarity matrix. Maximum diffuse attenuation (Damax), maximum photosynthetically active radiation (Par), pH, phosphate, Salinity, and mean sea surface temperature (Sstmean).

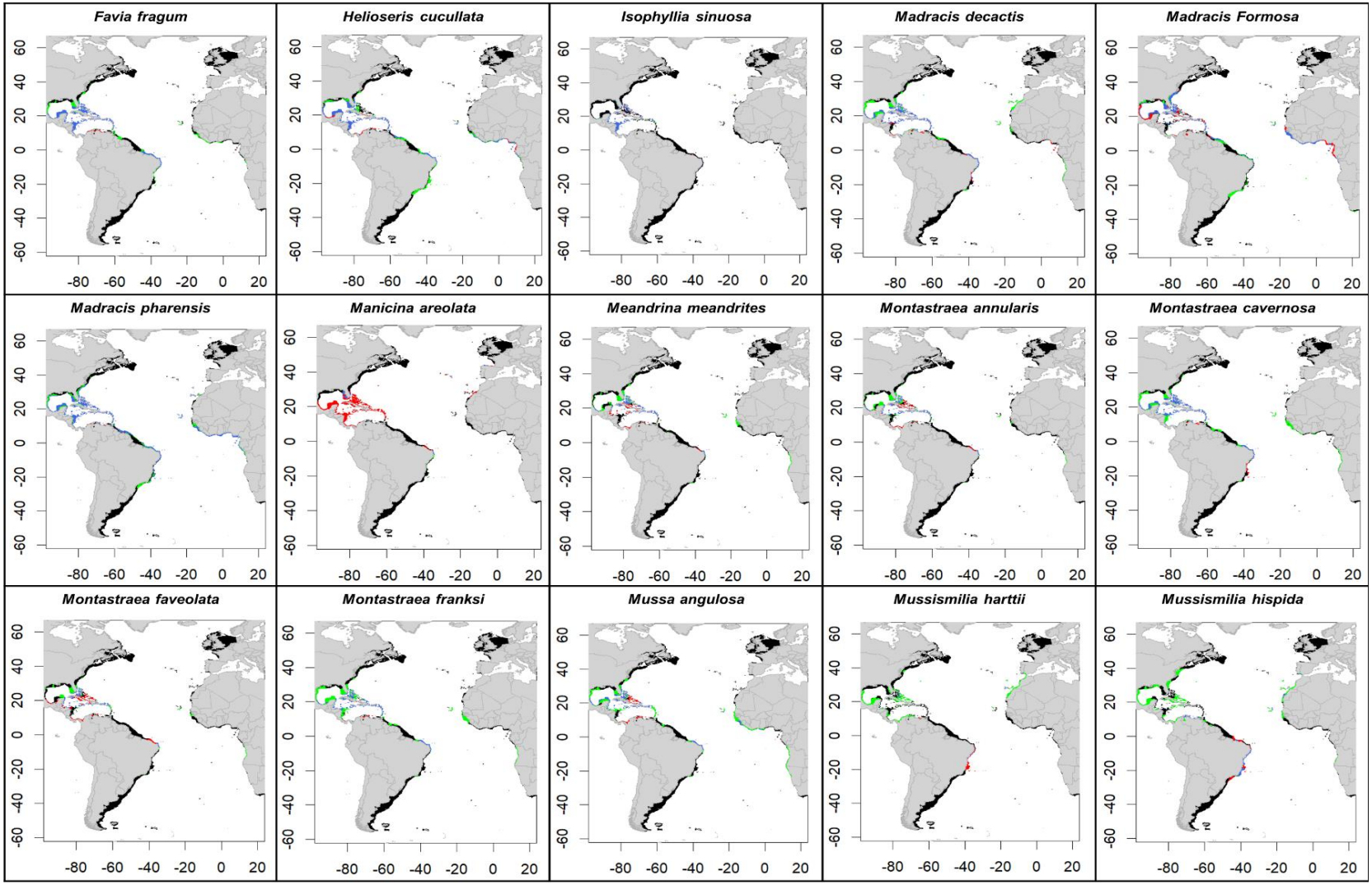
Variable	rho	p-value
Damax	0.095	0.02
Parmax	0.088	0.04
pH	0.111	0.01
Phosphate	0.088	0.04
Salinity	0.063	0.09
Sstmean	0.059	0.10

Table S4. Evolutionary distinctiveness (ED) of scleractinian Atlantic corals.

Ranking	Species	ED	Ranking	Species	ED
1	*Stephanocoenia intersepta*	246.4	**24**	*Porites branneri*	22.1
2	*Porites astreoides*	158.9	**25**	*Porites furcata*	22.1
3	*Madracis formosa*	130.7	**26**	*Montastraea annularis*	20.7
4	*Helioseris cucullata*	118.2	**27**	*Montastraea faveolata*	20.7
5	*Montastraea cavernosa*	115.3	**28**	*Agaricia agaricites*	17.6
6	*Siderastrea siderea*	109.0	**29**	*Agaricia tenuifolia*	17.6
7	*Siderastrea radians*	109.0	**30**	*Mussismilia harttii*	12.9
8	*Acropora cervicornis*	89.8	**31**	*Isophyllia sinuosa*	12.6
9	*Acropora palmata*	89.8	**32**	*Agaricia fragilis*	9.8
10	*Porites colonensis*	82.9	**33**	*Agaricia lamarcki*	9.8
11	*Solenastrea bournoni*	70.1	**34**	*Agaricia grahamae*	9.4
12	*Madracis pharensis*	66.2	**35**	*Agaricia undata*	9.4
13	*Madracis decactis*	66.2	**36**	*Mussismilia hispida*	8.6
14	*Agaricia humilis*	62.9	**37**	*Mycetophyllia danaana*	7.5
15	*Dendrogyra cylindrus*	62.9	**38**	*Favia fragum*	5.6
16	*Mussa angulosa*	47.8	**39**	*Mycetophyllia aliciae*	4.4
17	*Porites porites*	42.8	**40**	*Mycetophyllia lamarckiana*	4.4
18	*Montastraea franksi*	41.2	**41**	*Diploria labyrinthiformis*	3.6
19	*Solenastrea hyades*	37.0	**42**	*Diploria clivosa*	1.4
20	*Oculina varicosa*	37.0	**43**	*Diploria strigosa*	1.4
21	*Eusmilia fastigiata*	32.1	**44**	*Manicina areolata*	1.3
22	*Meandrina meandrites*	32.1	**45**	*Colpophyllia natans*	1.3
23	*Scolymia cubensis*	29.9			

Fig. S1. Expansion/contraction maps of scleractinian Atlantic corals. Expansions (green), contractions (red) and no change (blue) between 'current' and A2 2100 scenarios.




Favia fragum
Helioseris cucullata
Isophyllia sinuosa
Madracis decactis
Madracis Formosa
Madracis pharensis
Manicina areolata
Meandrina meandrites
Montastraea annularis
Montastraea cavernosa
Montastraea faveolata
Montastraea franksi
Mussa angulosa
Mussismilia harttii
Mussismilia hispida

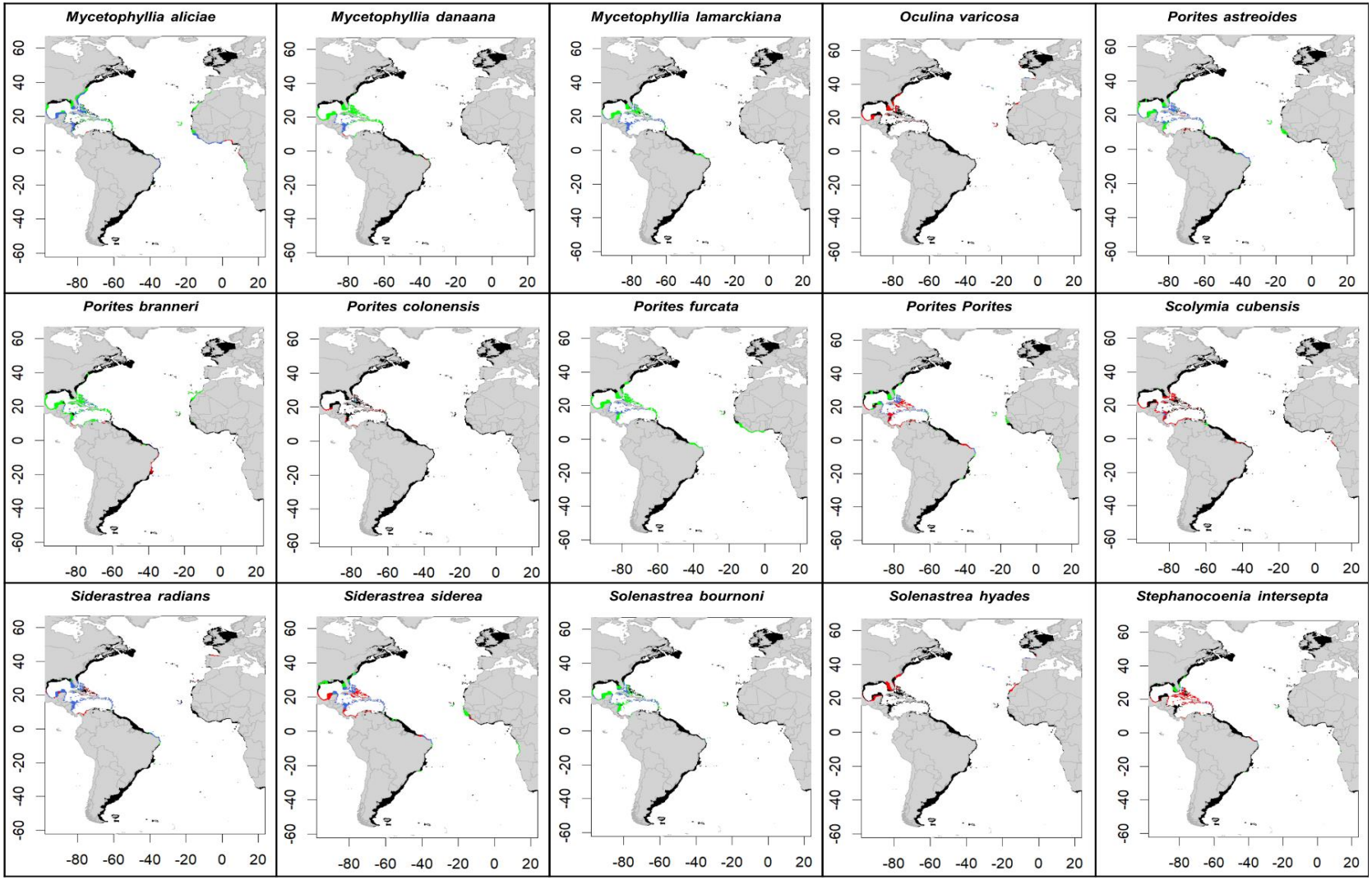

Mycetophyllia aliciae
Mycetophyllia danaana
Mycetophyllia lamarckiana
Oculina varicosa
Porites astreoides
Porites branneri
Porites colonensis
Porites furcata
Porites Porites
Scolymia cubensis
Siderastrea radians
Siderastrea siderea
Solenastrea bournoni
Solenastrea hyades
Stephanocoenia intersepta

Fig. S2. Projected mean sea surface temperature by the year 2100, according to the IPCC A2 scenario.

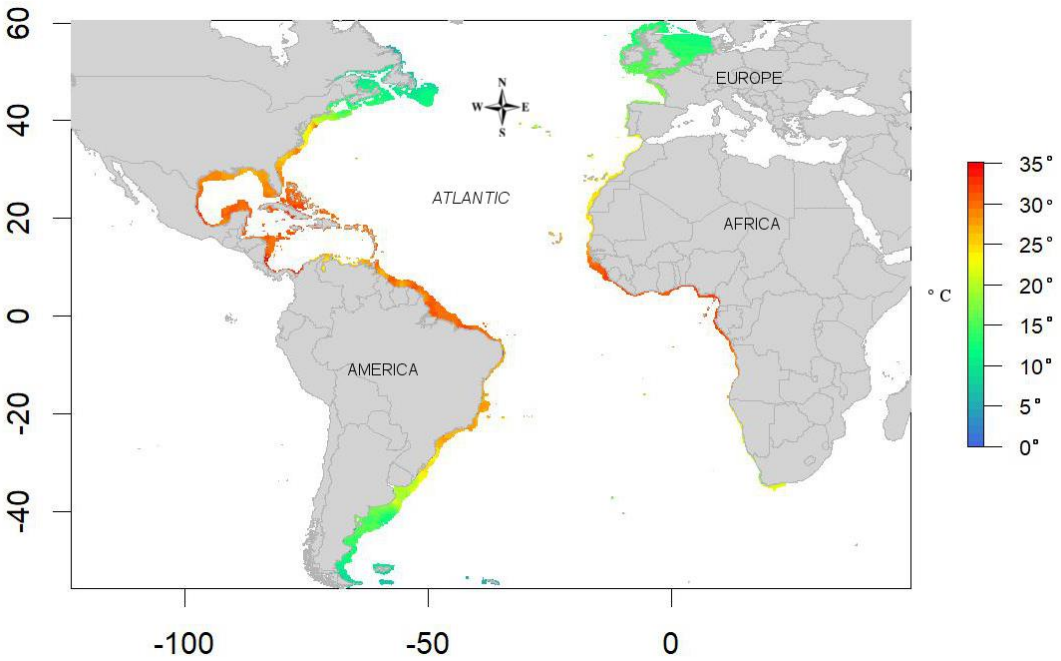
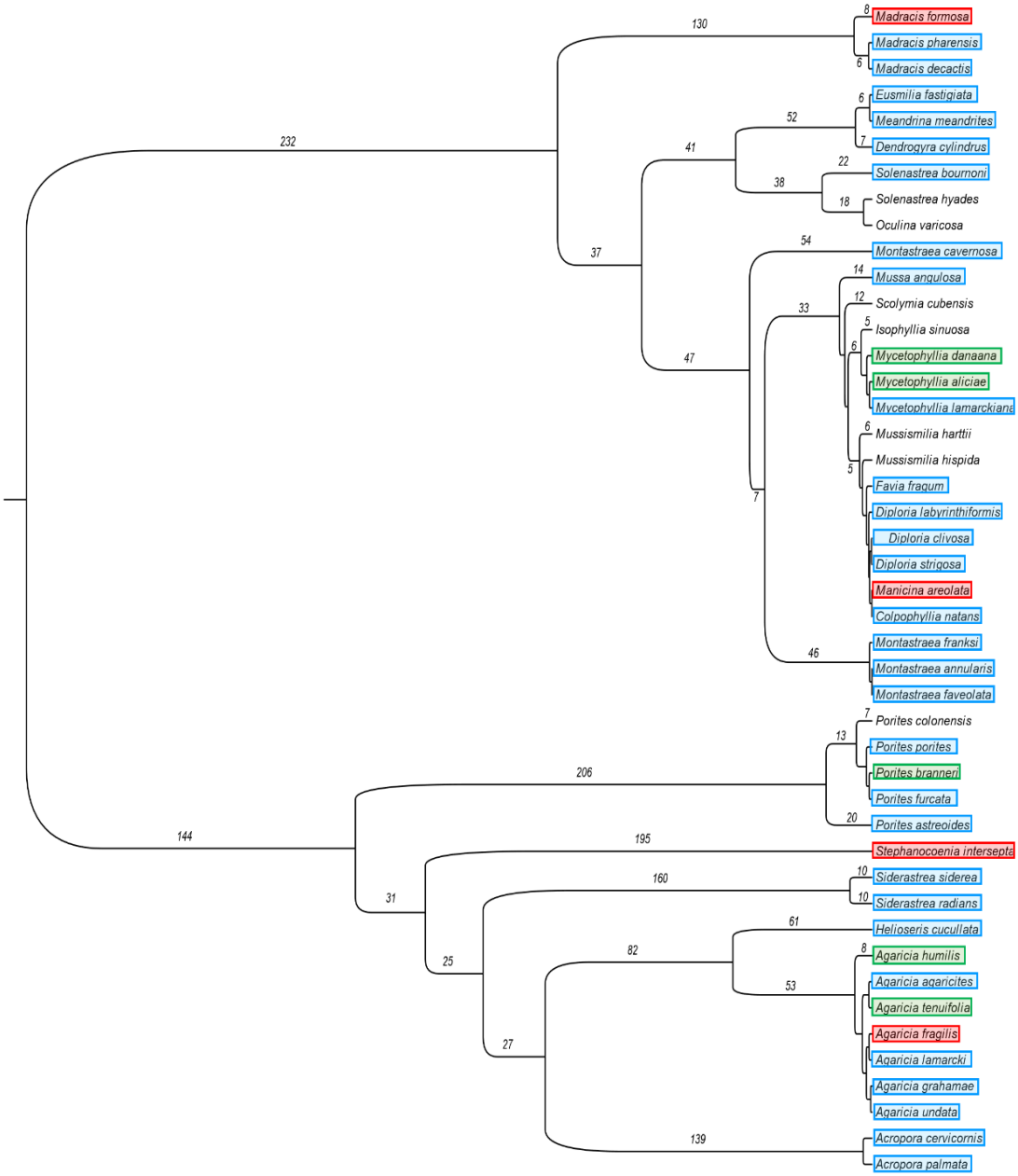


Fig. S3 Phylogenetic tree of coral species for the south of the Dominican Republic, according to the SDM predictions. Numbers indicate branch lengths (values <5 were omitted). In blue, species that appear in both 'current' and 'future' scenarios. In green, species that are absent under 'current' conditions, but appear under 'future' conditions (new presence). In red, species that are present under 'current' conditions, but disappear under 'future' conditions (new absence). Species that do not appear in either scenarios are not highlighted.



- Supplementary materials Chapter 4: Integration of physiological knowledge into Hybrid Species Distribution Modelling to improve forecast of distributional shifts of tropical corals

Table S1. Environmental variables extracted from Bio-Oracle.

Acronym	Variable	Units
Calcite [a]	Calcite concentration	mol/m2
Chlomax [a]	Max chlorophyll A concentration	mg/m^2
Chlomean [a]	Mean chlorophyll A concentration	mg/m^2
Chlomin [a]	Min chlorophyll A concentration	mg/m^2
Chlorange [a]	Chlorophyll A range	mg/m^2
Cloudmax [b]	Max cloud cover	%
Cloudmean [b]	Mean cloud cover	%
Cloudmin [b]	Min cloud cover	%
Damax [a]	Max diffuse attenuation (turbidity of the water column)	1/m
Damean [a]	Mean diffuse attenuation	1/m
Damin [a]	Min diffuse attenuation	1/m
Dissox [c]	Dissolved oxygen	ml/L
Nitrate [c]	Nitrate	µmol/L
Parmax [d]	Max photosynthetically available radiation	$Einstein/m^2/day$
Parmean [d]	Mean photosynthetically available radiation	$Einstein/m^2/day$
pH [c]	pH	-
Phosphate [c]	Phosphate	µmol/L
Salinity [c]	Salinity	PSS
Silicate [c]	Silicate	µmol/L
Sstmax [a]	Max sea surface temperature	°C
Sstmean [a]	Mean sea surface temperature	°C
Sstmin [a]	Min sea surface temperature	°C
Sstrange [a]	Range of sea surface temperature	°C

Bio-ORACLE layers derived from: [a] seasonal climatologies (2002–2009) obtained by the Aqua-MODIS satellite; [b] from monthly images (2005–2010) acquired by Terra-MODIS; [c] processed by DIVA interpolation for in-situ measurements from the World Ocean Database 2009 (WOD09) (Boyer et al., 2009); [d] photosynthetically available radiation from monthly climatologies (1997–2009) from the SeaWiFS satellite sensor. Original resolution: 5 arcmin (~9.2km). The layers were constrained by a bathymetric mask (BODC, 2003) to a depth of 100m in order to exclude deep waters with unsuitable seabed conditions for the modelled organism.

Table S2. Contribution of each environmental variable to the Correlative model using tree different fitting algorithms. In bold indicated the variables selected for the final models. Percentages > 20% shown in cursive.

Variable	MaxEnt	GLM biomod2	Random Forest
	Percent contribution* (%)	Variable importance^{+} (%)	IncMSE^{++} (%)
Sstmean	*62.1*	*65.0*	*22.0*
Salinity	*26.5*	*29.0*	*24.7*
pH	7.8	*25.9*	18.5
Damax	2.1	5.0	8.2
Parmax	1	6.6	6.0
Nitrate	0.5	0.0	5.7

* Percent contribution calculated with MaxEnt.

$^{+}$ Variable importance from the GLM fit with biomod2.

$^{++}$ Mean Squared Error Increment (IncMSE) for Random Forest.

Table S3. Left side: percentage of area classified as presence and absence for the current and the three IPCC scenarios for the year 2100 (B1, A1B and A2). Right side: percentage of area classified as new presence (increase) and new absence (decrease) in the future climatic scenarios with respect to the projections for the current scenario. All the percentages were calculated for the Correlative, Physiological and Hybrid models. The A2 scenario was chosen to explain the results.

Model	Scenario	Category of area		Scenario	Category of area changed	
		Presence (%)	Absence (%)		New presence (%)	New absence (%)
Correlative	*Current*	*29.6*	*70.4*	-	-	-
	B1	35.3	64.7	B1-current	11.6	1.5
	A1B	38.2	61.8	A1B-current	14.1	0.8
	A2	38.7	61.3	A2-current	14.8	0.9
Physiological	*Current*	*52.4*	*47.6*	-	-	-
	B1	50.8	49.2	B1-current	5.9	1.3
	A1B	48.8	51.2	A1B-current	6.7	4.3
	A2	48.9	51.1	A2-current	8.3	5.7
Hybrid	*Current*	*68.7*	*31.3*	-	-	-
	B1	35.4	64.6	B1-current	10.5	2.1
	A1B	37.0	63.0	A1B-current	12.5	2.3
	A2	35.7	64.3	A2-current	12.0	3.2

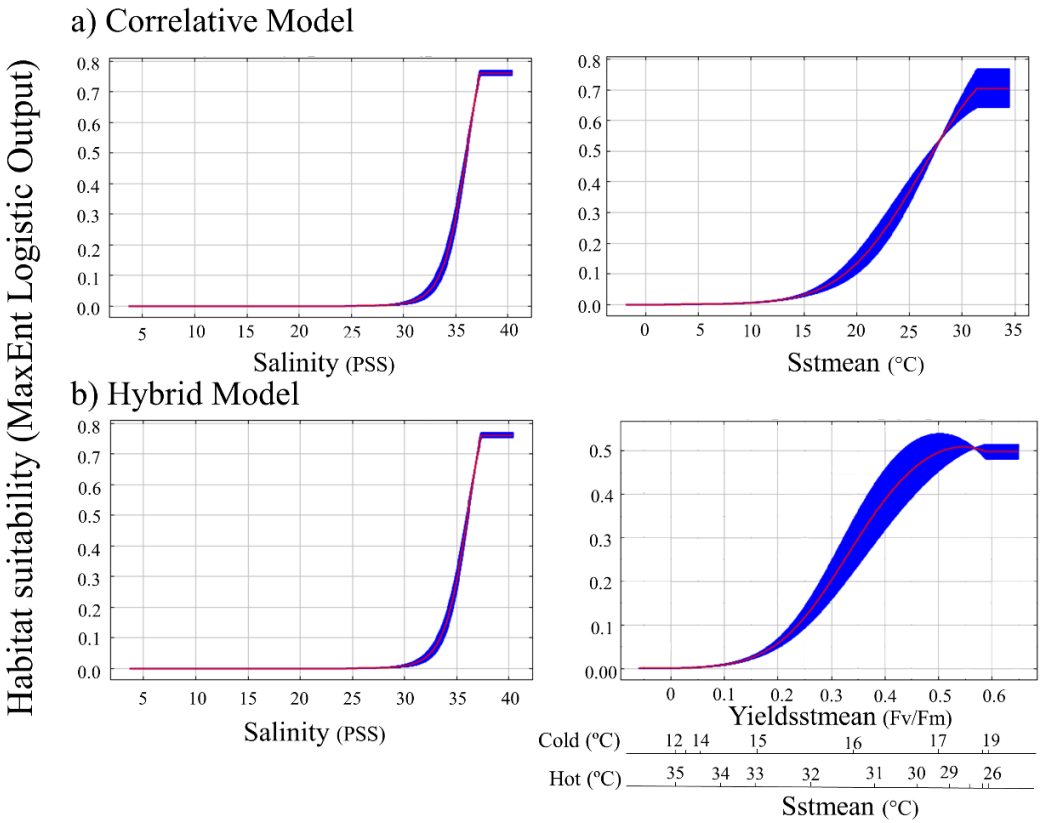


Fig. S1. MaxEnt response curves to the environmental predictors for: a) the Correlative model, and b) the Hybrid model. Red lines indicate the mean logistic habitat suitability, and the blue area shows the mean logistic habitat suitability ± one standard deviation based on 10 replicate runs.

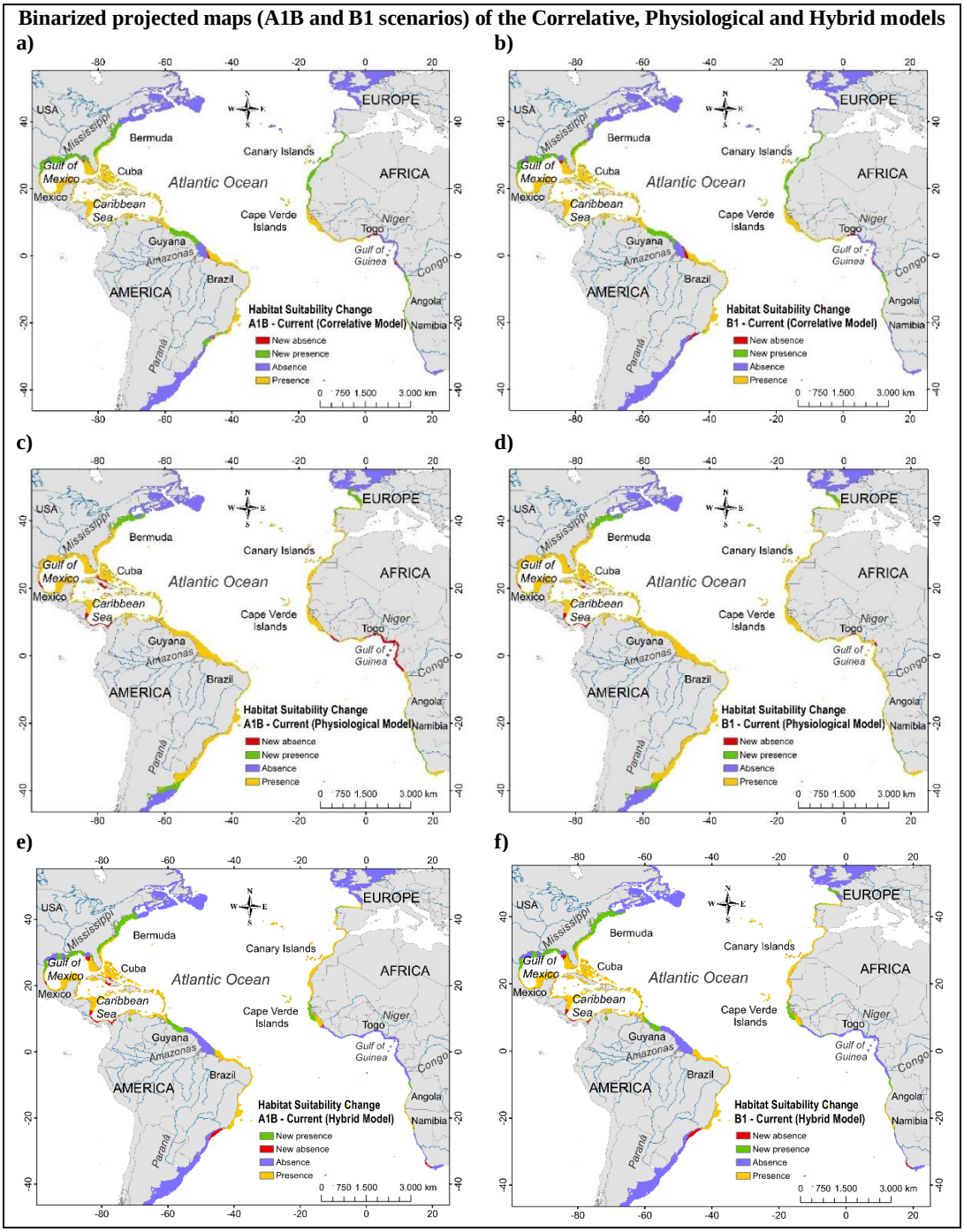


Fig. S2. Projected maps of the potential changes in habitat suitability in the future IPCC climatic scenario of A1B (left column) and B1 (right column) for the year 2100 compared to the current scenario, by applying the Correlative (a and b), Physiological (c and d) and Hybrid models (e and f), using 10 replicates in MaxEnt to obtain mean values for the Correlative and Hybrid models, and the physiological response curve in the Physiological model. Current and future habitat suitability values were transformed into presence (in blue) and absence areas (in black) using the threshold of Maximum Test Sensitivity Plus Specificity in Correlative models (A1B=0.29, B1=0.31) and Hybrid models (A1B=B1=0.33); and the threshold Fv/Fm value of 0.3 in Physiological models. New areas of future potential presence, in relation to the current climate, are shown in green, and in red new future areas of potential absence. (Symbols and legends as in Fig. 2).

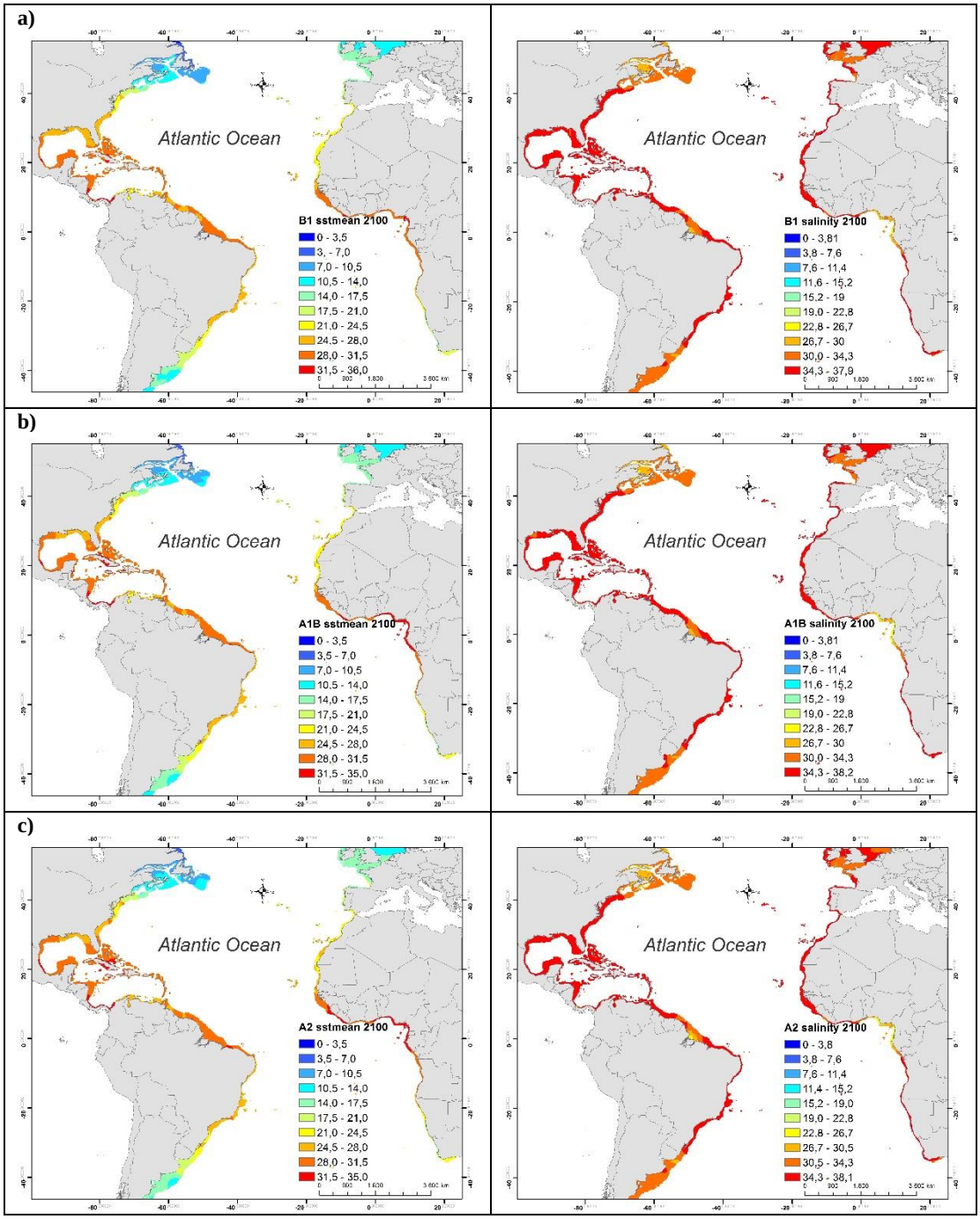


Fig. S3. Future Sstmean (left panel) and Salinity maps (right panel) for the three IPCC scenarios. a) B1, b) A1B, c) A2.

- Supplementary materials Chapter 5: Genetic relationships of the hydrocoral *Millepora alcicornis* and its symbionts within and between locations across the Atlantic

Table S1. Sample codes of *M. alcicornis* across the Atlantic (Cape Verde Islands, Spain, Mexico and Puerto Rico), including locations, dates and depth. GenBank accession number represents the coral samples correctly amplified by the 16S-rDNA and COI regions used in the analyses. In parenthesis (A) *Symbiodinium* sp., (B) *Breviolum* sp. and (C) *Cladocopium* sp. according to ITS and 23S-rDNA regions.

							M. alcicornis		Symbiont (genus)	
Sample	id	Country	Location	Site	Date	Depth (m)	16S	COI	ITS	23S
1	CV1	Cape Verde	Santiago	Cho Born	jul-2013	12-14		LN627008		
2	CV2	Cape Verde	Santiago	Cho Born	jul-2013	12-14		LN627011		MH673822 (B)
3	CV3	Cape Verde	Santiago	Cho Born	jul-2013	12-14				
4	CV4	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687300	LN627008		MH673826 (B)
5	CV5	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687302	LN627013	MH818383 (B)	MH673829 (B)
6	CV6	Cape Verde	Santiago	Cho Born	jul-2013	12-14		LN627010		MH673830 (B)
7	CV7	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687303	LN627014	MH818385 (B)	MH673831 (B)
8	CV8	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687305	LN627008		MH673833 (B)
9	CV9	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687306	LN627015		MH673834 (B)
10	CV10	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687307	LN627009		
11	CV11	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687308	LN627008		MH673835 (B)
12	CV12	Cape Verde	Santiago	Cho Born	jul-2013	12-14		LN627009		MH673837 (B)
13	CV13	Cape Verde	Santiago	Cho Born	jul-2013	12-14	MH687309	LN627010		
14	CV14	Cape Verde	Santiago	3 Piedras	jul-2013	10-12		LN627008		MH673839 (B)
15	CV15	Cape Verde	Santiago	3 Piedras	jul-2013	10-12	MH687310	LN627008	MH818387 (B)	MH673840 (B)
16	CV16	Cape Verde	Santiago	3 Piedras	jul-2013	10-12	MH687311	LN627008		MH673842 (B)
17	CV17	Cape Verde	Santiago	3 Piedras	jul-2013	10-12	MH687312	LN627008		
18	CV18	Cape Verde	Santiago	3 Piedras	jul-2013	10-12	MH687314	LN627008	MH818390 (C)	MH673845 (B)
19	CV20	Cape Verde	Santiago	3 Piedras	jul-2013	10-12	MH687315	LN627008	MH818392 (C)	MH673846 (B)
20	CN21	Spain	Tenerife	Porís	ago-2013	3-8	MH687316	LN627012	MH818393 (C)	MH673847 (B)

Sample	id	Country	Location	Site	Date	Depth (m)	16S	COI	ITS	23S
21	CN22	Spain	Tenerife	Porís	ago-2013	3-8	MH687317	LN627012		MH673848 (B)
22	CN23	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
23	CN24	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
24	CN25	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
25	CN26	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
26	CN27	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
27	CN28	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
28	CN29	Spain	Tenerife	Porís	ago-2013	3-8		LN627012		
29	CVD1	Cape Verde	Sao Vicente	Islote	ene-2014	8-10	MH687329	LN627008		
30	CVD2	Cape Verde	Sao Vicente	Islote	ene-2014	8-10	MH687330	LN627008		
31	CVD3	Cape Verde	Sao Vicente	Islote	ene-2014	8-10	MH687331	LN627008		
32	CVD4	Cape Verde	Sao Vicente	Islote	ene-2014	8-10	MH687332	LN627017		
33	CVD5	Cape Verde	Sao Vicente	Islote	ene-2014	8-10	MH687333	LN627008	MH818397 (B)	
34	CVD6	Cape Verde	Sao Vicente	Islote	ene-2014	8-10	MH687334	LN627008		
35	CVB1	Cape Verde	Sao Vicente	Baia das Gatas	ene-2014	1-2	MH687323	LN627008		
36	CVB2	Cape Verde	Sao Vicente	Baia das Gatas	ene-2014	1-2	MH687324	LN627008	MH818396 (B)	
37	CVB3	Cape Verde	Sao Vicente	Baia das Gatas	ene-2014	1-2	MH687325	LN627008		
38	CVB4	Cape Verde	Sao Vicente	Baia das Gatas	ene-2014	1-2	MH687326	LN627016		
39	CVB5	Cape Verde	Sao Vicente	Baia das Gatas	ene-2014	1-2	MH687327	LN627008		
40	CVB6	Cape Verde	Sao Vicente	Baia das Gatas	ene-2014	1-2	MH687328	LN627010		
41	CV50	Cape Verde	Sal	B. Murdeira	jul-2014	low intertidal	MH687318	MK034165	MH818394 (B)	MH673849 (B)
42	CV51	Cape Verde	Sal	B. Murdeira	jul-2014	low intertidal	MH687319	MK034166	MH818395 (B)	
43	CV52	Cape Verde	Sal	B. Murdeira	jul-2014	low intertidal	MH687320	MK034167		MH673850 (B)
44	CV53	Cape Verde	Sal	B. Murdeira	jul-2014	8-10	MH687321	MK034168		
45	CV54	Cape Verde	Sal	B. Murdeira	jul-2014	8-10				MH673851 (B)
46	CV55	Cape Verde	Sal	B. Murdeira	jul-2014	8-10	MH687322	MK034169		MH673852 (B)
47	1R	Mexico	Puerto Morelos	La Bocana Reef	sep-2015	3-5	MH687298	MH665225	MH818378 (A)	MH673821 (A)

Sample	id	Country	Location	Site	Date	Depth (m)	16S	COI	ITS	23S
48	2R	Mexico	Puerto Morelos	La Bocana Reef	sep-2015	3-5	MH687299	MH665228	MH818380 (A)	MH673825 (A)
49	7R	Mexico	Puerto Morelos	La Bocana Reef	sep-2015	3-5	MH687304	MH665230	MH818386 (A)	MH673832 (A)
50	1Ds	Mexico	Puerto Morelos	La Bocana Reef	sep-2015	3-5	MH687296	MH665223	MH818376 (A)	MH673819 (A)
51	2Ds	Mexico	Puerto Morelos	La Bocana Reef	sep-2015	3-5		MH665226		MH673823 (A)
52	4Ds	Mexico	Puerto Morelos	La Bocana Reef	sep-2015	3-5	MH687301	MH665229	MH818382 (A)	MH673828 (A)
53	1M	Mexico	Puerto Morelos	Pier UNAM (right side)	sep-2015	1-2	MH687297	MH665224	MH818377 (A)	MH673820 (A)
54	2P	Mexico	Puerto Morelos	Pier UNAM (left side)	sep-2015	1-3		MH665227	MH818379 (A)	MH673824 (A)
55	4EM	Puerto Rico	La Parguera	El Mario Reef	unknown	2-7	MH687335		MH818381 (B)	MH673827 (A)
56	6M	Puerto Rico	La Parguera	Margarita Reef	feb-2015	1-5	MH687336		MH818384 (B)	
57	11P	Puerto Rico	La Parguera	Pelotas Reef	oct-2015	1-5	MH687339	MH665231	B	MH673836 (A)
58	13E	Puerto Rico	La Parguera	Enrique Reef	dic-2012	2				MH673838 (A)
59	15T	Puerto Rico	La Parguera	Turrumote Reef	oct-2008	1-5			MH818388 (B)	MH673841 (A)
60	16ML	Puerto Rico	La Parguera	Media Luna Reef	sep-2015	2	MH687337			MH673843 (A)
61	17ML	Puerto Rico	La Parguera	Media Luna Reef	sep-2013	2	MH687313		MH818389 (B)	MH673844 (A)
62	18ML	Puerto Rico	La Parguera	Media Luna Reef	ene-2015	2	MH687338		MH818391 (B)	

Table S2. GenBank sequences included in the 16S and COI analyses.

Region	Site	GenBank accession number	Reference
16S-rDNA	Caribbean Province, Bermuda	KT891016	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Bermuda	KT891017	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Bermuda	KT891018	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Panama	KT891025	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Panama	KT891026	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Panama	KT891027	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Florida	KT891032	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Florida	KT891033	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Florida	KT891034	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Colombia	KT891049	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Colombia	KT891050	(de Souza et al., 2017)
16S-rDNA	Caribbean Province, Colombia	KT891051	(de Souza et al., 2017)
16S-rDNA	Ascension Province, Ascension Island	KT891060	(de Souza et al., 2017)
16S-rDNA	Ascension Province, Ascension Island	KT891061	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Fernando de Noronha	KT891072	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Fernando de Noronha	KT891073	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Rio Grande do Norte	KT891087	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Rio Grande do Norte	KT891088	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Pernambuco	KT891096	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Pernambuco	KT891097	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Southern Alagoas (Maceió)	KT891101	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Southern Alagoas (Maceió)	KT891102	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Northern Bahia (Salvador)	KT891107	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Northern Bahia (Salvador)	KT891108	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Southern Bahia (Porto Seguro)	KT891131	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Southern Bahia (Porto Seguro)	KT891132	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Espírito Santo	KT891151	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Espírito Santo	KT891152	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Rio de Janeiro	KT891171	(de Souza et al., 2017)
16S-rDNA	Brazilian Province, Rio de Janeiro	KT891172	(de Souza et al., 2017)
COI	La Parguera, Puerto Rico	511534929	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534931	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534937	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534941	(Ruiz-Ramos et al., 2014)

COI	La Parguera, Puerto Rico	511534943	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534945	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534947	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534983	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534989	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511534993	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535001	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535011	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535015	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535017	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535025	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535029	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535031	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535035	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535043	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535059	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535067	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535093	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535123	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535129	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535133	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535167	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535209	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535213	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535221	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535237	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535241	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535259	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535275	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535303	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535315	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535327	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535329	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535333	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535337	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535343	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535345	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535369	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535373	(Ruiz-Ramos et al., 2014)

COI	La Parguera, Puerto Rico	511535375	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535379	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535393	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535407	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535421	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535455	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535463	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535473	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535485	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535515	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535533	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535537	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535539	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535541	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535553	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535555	(Ruiz-Ramos et al., 2014)
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COI	La Parguera, Puerto Rico	511535587	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535589	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535591	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535595	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535603	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535613	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535619	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535635	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535637	(Ruiz-Ramos et al., 2014)
COI	La Parguera, Puerto Rico	511535667	(Ruiz-Ramos et al., 2014)

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Fig. S1. Phylogenetic analyses inferred from ITS2 including a) *Breviolum* spp. (subclades B), b) *Symbiodinium* spp. (Subclades A) and c) *Cladocopium* spp. (Subclades C).